



Nutritional Ecology of Elk During Summer and Autumn in the Pacific Northwest

JOHN G. COOK,¹ *National Council for Air and Stream Improvement, Forestry and Range Science Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA*

RACHEL C. COOK, *National Council for Air and Stream Improvement, Forestry and Range Science Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA*

RONALD W. DAVIS,² *Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61820, USA*

LARRY L. IRWIN, *National Council for Air and Stream Improvement, P.O. Box 68, Stevensville, MT 59870, USA*

ABSTRACT Elk (*Cervus elaphus*) in the western United States are an economically and socially valuable wildlife species. They have featured species status for federal land management planning; hence, considerable modeling focused on habitat evaluation and land management planning has been undertaken for elk. The extent to which these and other habitat models for large ungulates account for influences of nutritional resources varies greatly, probably because of varying recognition of the importance of nutrition and uncertainty about how to measure and model nutrition. Our primary goals were to 1) develop greater understanding of how habitat conditions influence foraging dynamics and nutrition of elk in summer and autumn; and 2) illustrate an ecological framework for evaluating and predicting nutritional resources so that nutritional needs of elk can be integrated within landscape-scale plans, population models, and habitat evaluation models. We evaluated foraging responses of elk to clearcut logging and commercial thinning, forest succession, and season across ecological site potentials. We also identified the extent to which plant communities satisfied nutritional requirements of lactating female elk and their calves. Our study was conducted in the temperate rainforests of the Pacific Northwest on industrial and public timberlands.

We evaluated relations between habitat conditions and elk nutrition in plant communities representing a range in stand age and ecological conditions at 3 study areas, 1 near the Canadian border in the north Cascades Mountains (Nooksack), 1 in the Coast range southwest of Olympia, Washington (Willapa Hills), and the third in the central Cascades near Springfield, Oregon (Springfield), from late June to November, 2000–2002. In 98–143 macroplots per study area, we measured forage abundance by plant species, digestible energy content by plant life-form group, and forest overstory. In a subset of these macroplots (~30 per study area), we held 4 tame lactating elk with calves in electrified pens ($n = 15$ –25 adult elk per year), and sampled activity budgets, dietary composition, forage selection, and other measures of foraging behavior; dietary digestible energy (DE; kcal/g) and protein (DP; %) levels; and intake rates of these nutrients. In 15 of these pens, we held elk for extended periods (13–21 days) to monitor changes in body fat of adults and growth of calves. We developed equations to predict dietary DE and DP and per-minute intake rates of each in a nutrition prediction model that reflected vegetation attributes and ecological site influences.

Total abundance of forage in the western hemlock series after clearcut logging in low to moderate elevations ($\leq 1,000$ m) ranged from a peak of 3,000–4,500 kg/ha in 5- to 10-year-old stands to 100–300 kg/ha in 20- to 50-year-old stands with only moderate increases through late succession. Patterns were similar in higher elevation forests (1,000–1,800 m), although peaks and troughs in forage abundance developed more slowly. Deciduous shrubs, forbs, and graminoids were abundant in early seral stages after stand disturbance, but these were rapidly replaced by shade-tolerant evergreen shrubs and ferns as conifer overstories closed 15–20 years later in low-elevation forest zones, and 20–40 years later in high-elevation zones. Digestible energy within plant life-form groups generally declined with season and with advancing succession, increased with elevation, and was highest in forbs and deciduous shrubs and lowest in evergreen shrubs and shade-tolerant ferns.

Levels of DE in elk diets exhibited a strong asymptotic relation with abundance (kg/ha) of plant species that were eaten in proportions equal to or greater than availability (i.e., accepted species). Marked declines in dietary DE occurred in stands containing <400 kg/ha to 500 kg/ha of accepted species, largely because elk began to increase consumption of avoided species, and these typically contained low levels of DE. The asymptotic pattern was generally consistent among seasons, study areas, and habitat types (potential natural vegetation categories), although the asymptote averaged 10–12% greater in high- versus low-elevation forests. Abundance of accepted species in early seral stands averaged 7–10 times that in mid and late seral stages, and dietary DE levels varied accordingly. Dietary DE was little influenced by thinning in 20- to 60-year-old stands. In contrast, levels of dietary DP were unrelated to forage composition and abundance of accepted or avoided species, and varied little between

Received: 3 April 2013; Accepted: 1 July 2016

¹E-mail: cookjg.ncasi@gmail.com

²Present address: Natural Resource Conservation Management, Western Carolina University, Cullowhee, North Carolina, 28723, USA.

low and high-elevation forests. Dietary DP increased with overstory canopy cover, was higher in thinned and hardwood stands, particularly those hardwood stands with saturated soils in late summer, declined with season, and was lowest in the driest forest communities in our study. Overall, soil moisture regime and season accounted for the majority of variation in dietary DP.

Relations between nutrient intake rate and vegetation conditions varied among study areas and habitat types. Nevertheless, elk maintained about double the intake rate of DE in early seral stages versus closed-canopy forests. Intake rate of DP was similar between early seral versus closed-canopy forests, despite modestly lower dietary DP in early seral stages. Protein intake rate was greater in thinned and hardwood-riparian stands. In early seral stages, dietary DE typically met the requirement of 2.7 kcal/g of ingested forage (necessary to maintain body fat levels of lactating elk in summer) in the low-elevation forest zones and exceeded that level in high-elevation forest zones. In closed-canopy forests, dietary DE averaged below requirements, markedly so in low-elevation forests (2.25–2.5 kcal/g) and moderately so in high-elevation forests (2.4–2.65 kcal/g). Evidence of deficiencies based on DE intake rate was greater, averaging about 50% of requirements (28 kcal/min; 21,000 kcal/day) in closed-canopy forests and 80% of requirements in early seral stages. In contrast, dietary DP and DP intake rates generally approached or exceeded estimated requirements (6.8% DP; 380 g/day) in many habitat types that we sampled, with the greatest potential for deficient DP intake rates in relatively dry, low-elevation forests.

Body fat dynamics and growth of calves confirmed nutritional deficiencies suggested by our data on DE intake. Adult elk lost body fat during all trials at rates generally in accordance with expectations at the dietary DE levels they consumed, and rate of change in body fat was inversely related to abundance of accepted species. Calves grew at about half the rate of which they are capable (1 kg/day) if summer nutrition is sufficient. Daily calf growth was positively related to their mother's dietary DE and protein intake levels.

Elk compensated for limited foraging options in many plant communities via several behavioral strategies. Selection was generally strong for plants with higher DE levels, where selected species composed nearly 5 times more of the diet than did species that elk avoided, yet avoided species were 10 times more abundant. As abundance of accepted species declined below approximately 400 kg/ha, elk increased intake of avoided species. This strategy delayed declines in per-minute forage and DE intake rate as long as abundance of accepted species remained above roughly 200 kg/ha, despite declining dietary DE levels apparent at <400 kg/ha to 500 kg/ha of accepted species. Elk traveled faster while foraging to compensate for plant communities with very low abundance of total forage, increased bite rate as bite mass declined, increased time spent feeding at night in pens with low abundance of total forage or relatively low dietary DE levels, and increased rumination time particularly as dietary fiber levels increased. Dietary DE, DP, and intake rates of these nutrients therefore were robust to substantial variation in overall forage quality and quantity. Nevertheless, these strategies were insufficient to compensate for low abundance of high-quality forage typically present under closed forest canopies.

Our nutrition model included nonlinear and multiple regression equations to predict 1) dietary DE (kcal/g of ingested forage), based primarily on abundance of accepted species ($r^2 = 0.49$ – 0.62); and 2) dietary DP (% of ingested forage), based primarily on abundance of accepted species, overstory canopy cover, and site characteristics intended to index soil moisture ($r^2 = 0.60$). Additional equations to predict intake rates per minute included the same covariates, but the variance explained was modestly lower (DE intake: $r^2 = 0.43$; DP intake: $r^2 = 0.45$ – 0.54). With these equations, we created nutrition-succession profiles to illustrate dietary DE and DP intake dynamics across the successional sequence for each habitat type and study area. These profiles may serve as inputs for spatially explicit maps of nutritional resources for elk. Because they were developed using nutrition data from foraging elk, they should help alleviate much of the uncertainty arising from proxy variables often used as indices of nutritional resources.

Our data demonstrated that nutritional resources in forests of western Oregon and Washington are generally deficient for lactating elk in summer and early autumn. They provided evidence that inadequate nutritional resources are largely responsible for low body fat in autumn and reduced pregnancy rates reported for many elk herds in the Pacific Northwest. Our data also illustrated that nutritional value of habitats is highly variable depending on ecological context, disturbance, and succession. Thus, how, if, and where forested elk habitats are managed can greatly influence the nutritional suitability of an area. Finally, our data indicate a considerable need for integrating nutritional assessments in landscape planning processes where maintaining abundant and productive elk populations is one of several forest management goals in the Pacific Northwest. © 2016 The Wildlife Society.

KEY WORDS *Cervus elaphus*, digestible energy, disturbance, elk, habitat management, landscape planning, nutritional ecology, Pacific Northwest, protein, succession, summer.

Ecología Nutricional del Ciervo durante el Verano y el Otoño en el Pacífico Noroeste

RESUMEN En el oeste de los Estados Unidos, el ciervo (*Cervus elaphus*) es una especie silvestre de gran valor socioeconómico. A nivel federal, el ciervo es una especie *con* estatus destacado en la planificación del ordenamiento territorial. Por este motivo, numerosos trabajos de modelización se han centrado en la evaluación del hábitat del ciervo y la planificación del ordenamiento territorial en relación al ciervo. El grado en que estos y otros modelos de hábitat de grandes ungulados reflejan las influencias de los recursos nutricionales varía mucho, probablemente debido a la variada importancia acordada por los científicos a la alimentación y también a causa de la incertidumbre asociada a la manera de medir y modelizar la nutrición. Nuestros principales objetivos fueron: (1) comprender mejor cómo las condiciones del hábitat influyen la dinámica de búsqueda alimentaria, así como la alimentación del ciervo durante el verano y el otoño, y (2) elaborar un marco ecológico para evaluar y predecir recursos nutricionales de manera a integrar las necesidades nutricionales del ciervo a los planes a nivel de paisaje, a los modelos de población y a los modelos de evaluación del hábitat. Evaluamos cómo la deforestación y las actividades de aclareo comercial, las sucesiones forestales y las estaciones afectan al ciervo en su búsqueda alimentaria en varios lugares *con* potencial ecológico. También identificamos en qué medida las comunidades vegetales satisfacían las necesidades nutricionales de las hembras lactantes y la de sus crías. Nuestro estudio fue realizado en los bosques tropicales templados de la región del Noroeste del Pacífico, sobre tierras de producción maderera tanto industriales como públicas.

Evaluamos las relaciones entre las condiciones del hábitat y la alimentación del ciervo en comunidades vegetales *con* respecto a varias edades de masa forestal y condiciones ecológicas en 3 áreas de estudio, a saber, 1 cerca de la frontera canadiense en las Montañas de las Cascadas del Norte (Nooksack); 1 en la cadena costera al suroeste de Olympia, Washington (Willapa Hills); y 1 en la región central de la cordillera de las Cascadas cerca de Springfield, Oregón (Springfield), entre el fin del mes de junio y noviembre, 2000-2002. En cada área de estudio evaluamos 98-143 macro parcelas y medimos la abundancia del forraje por especie vegetal, el contenido energético digestible por grupo biológico de vegetales, y el piso dominante del bosque. En un subconjunto de estas macro parcelas (~30 por área de estudio), mantuvimos 4 hembras lactantes domesticadas, junto *con* sus crías, dentro de corrales electrificados ($n = 15-25$ ciervos adultos por año), y muestreamos los presupuestos de actividad, la composición dietética, la selección de forraje y otros índices asociados a la búsqueda alimentaria, los niveles dietéticos de energía digestible (ED; kcal/g) y de proteína digestible (PD; %), y las tasas de ingesta de ED y de PD. En cada área de estudio, mantuvimos a los ciervos en 5 de estos corrales por largos periodos (13-21 días) *con* el fin de monitorear cambios en la grasa corporal de los adultos y en el crecimiento de las crías. Desarrollamos ecuaciones para predecir los niveles dietéticos de ED y de PD, así como las tasas de ingesta por minuto de cada animal, y las incorporamos en un modelo predictivo nutricional que refleja atributos de la vegetación y las influencias ecológicas del lugar.

La abundancia total de forraje en la eco zona de la tsuga del Pacífico luego de la deforestación efectuada a bajas y moderadas altitudes ($\leq 1\,000$ m) varió desde un máximo de 3 000 a 4 500 kg/ha en masas forestales de 5 a 10 años, hasta niveles de 100 a 300 kg/ha en masas forestales de 20 a 50 años *con* sólo moderados aumentos hasta la última etapa de sucesión. Los patrones fueron similares en bosques situados a mayor altitud (1 000 a 1 800 m), aunque los altibajos en la abundancia del forraje se desarrollaron más lentamente. Los arbustos de hojas caducas, y las especies herbáceas y gramíneas fueron abundantes durante las primeras etapas de sucesión ecológica luego de las perturbaciones de la masa forestal, pero estas plantas fueron rápidamente remplazadas por arbustos de hoja perenne y helechos tolerantes a la sombra a medida que el piso dominante conífero se cerraba 15 a 20 años después en zonas forestales bajas, y 20 a 40 años después en zonas forestales altas. En general, la energía digestible en los grupos biológicos de vegetales declinó en función de las estaciones y a medida que la sucesión avanzaba; aumentó *con* la altura; y alcanzó los niveles más altos en las herbáceas y en los arbustos de hojas caducas y los más bajos en los arbustos de hoja perenne y en los helechos tolerantes a la sombra.

Los niveles de ED en las dietas de los ciervos exhibieron una fuerte relación asintótica *con* respecto a la abundancia de especies vegetales consumidas en proporciones iguales o mayores a su disponibilidad (es decir, las especies aceptadas). Disminuciones marcadas del nivel dietético de ED ocurrieron en masas forestales conteniendo menos de 400 kg/ha a 500 kg/ha de especies aceptadas, en gran medida debido a que los ciervos comenzaron a aumentar el consumo de especies evitadas. El patrón asintótico fue generalmente el mismo independientemente de la estación, el área de estudio y el tipo de hábitat (categorías de vegetación natural potencial), aun cuando la asíntota en bosques de gran altitud fue en promedio un 10-12% superior a la asíntota en bosques de baja altitud. Las especies aceptadas en las primeras etapas de sucesión ecológica fueron en promedio de 7 a 10 veces más abundantes que en las etapas intermedias y finales de sucesión, y los niveles dietéticos de ED variaron en consecuencia. El nivel dietético de ED fue influenciado muy poco por actividades de aclareo en masas forestales de 20 a 60 años. En cuanto a los niveles

dietéticos de PD, éstos no mostraron relación alguna *con* la composición del forraje ni *con* la abundancia de especies aceptadas y evitadas, y variaron muy poco *con* la altitud de los bosques. El nivel dietético de PD aumentó *con* la cubierta del piso dominante; fue mayor en masas forestales clareadas y de madera frondosa (en especial aquellas masas forestales de madera frondosa *con* suelos saturados durante la última parte del verano); disminuyó *con* las estaciones; y alcanzó su nivel más bajo en las comunidades forestales más secas evaluadas en nuestro estudio. En conjunto, el régimen de humedad del suelo y las estaciones explicaron la mayoría de las variaciones en los niveles dietéticos de PD.

Las relaciones entre las tasas de consumo de nutrientes y las condiciones de la vegetación variaron según el área de estudio y el tipo de hábitat. Sin embargo, los ciervos mantuvieron una tasa de ingesta de ED que fue cerca de dos veces más elevada en bosques en etapas tempranas de sucesión ecológica que en bosques de cubierta o dosel cerrado. Las tasas de ingesta de proteínas fueron mayores en masas forestales clareadas y ribereñas de madera frondosa. Durante las etapas tempranas de sucesión, los niveles dietéticos de ED correspondieron generalmente al requerimiento de 2,7 kcal/g de forraje consumido (necesario para mantener los niveles de grasa corporal de las hembras lactantes durante el verano) en zonas forestales bajas y excedieron ese nivel en zonas forestales altas. En bosques de cubierta cerrada, el nivel dietético de ED fue en promedio inferior al nivel necesario para satisfacer las necesidades de los ciervos, sobre todo en bosques de baja elevación (2,25–2,5 kcal/g) y en cierta medida en bosques situados a mayor altura (2,4–2,65 kcal/g). La tasa de ingesta de ED fue el parámetro que evidenció mayores deficiencias, promediando cerca de 50% del nivel requerido por los ciervos (28 kcal/min; 21 000 kcal/día) en bosques de cubierta cerrada y 80% del nivel requerido por los ciervos en bosques en etapas tempranas de sucesión. En cambio, los niveles dietéticos de PD y las tasas de ingesta de PD tendieron a aproximarse o a exceder los niveles requeridos por los ciervos (6,8% DP; 380 g/día) en varios de los tipos de hábitat que muestreamos. Los bosques relativamente secos y situados a baja altitud son altamente susceptibles de presentar deficiencias en la tasa de ingesta de PD.

La dinámica de la grasa corporal y el crecimiento de las crías confirmaron las deficiencias nutricionales que nuestros datos sobre el consumo de ED sugirieron. Los ciervos adultos perdieron grasa corporal durante todas las pruebas a tasas esperadas teniendo en cuenta los niveles dietéticos de ED que consumieron. La tasa de variación de la grasa corporal fue inversamente proporcional a la abundancia de las especies aceptadas. Las crías crecieron a un ritmo de aproximadamente la mitad de lo que son capaces (1 kg/día) cuando el aporte estival en nutrientes fue suficiente. El crecimiento diario de las crías estuvo directamente relacionado al nivel dietético de ED de la madre y al nivel de proteínas ingeridas por la misma.

Los ciervos compensaron las opciones limitadas para procurarse alimento que había en muchas comunidades vegetales adoptando diferentes estrategias de comportamiento. En general, su selección estaba centrada en plantas *con* altos niveles de ED. Estas especies vegetales formaron parte de la alimentación de los ciervos casi 5 veces más a menudo que las especies vegetales que evitaban ingerir, aun cuando las especies evitadas eran 10 veces más abundantes. Cuando la abundancia de las especies aceptadas disminuyó aproximadamente por debajo de 400 kg/ha, los ciervos aumentaron la ingesta de especies evitadas. Esta estrategia retardó la disminución de la tasa de consumo de forraje por minuto y la disminución de la tasa de ingesta de ED siempre que la abundancia de las especies aceptadas se mantuvo aproximadamente por encima de 200 kg/ha, aun a pesar de una disminución de los niveles dietéticos de ED que se hizo aparente cuando la abundancia de las especies aceptadas alcanzó niveles por debajo de 400 a 500 kg/ha. Los ciervos se desplazaron más rápidamente durante su búsqueda alimentaria *con* el fin de compensar la muy baja abundancia de forraje total en ciertas comunidades vegetales; aumentaron la tasa de bocado a medida que disminuía la masa de bocado; pasaron más tiempo en alimentarse durante la noche en corrales *con* poca abundancia de forraje total o *con* relativamente bajos niveles dietéticos de ED; e incrementaron el tiempo de rumia sobre todo cuando los niveles de fibra en la dieta aumentaron. En consecuencia, los niveles dietéticos de ED y de PD, y las tasas de consumo de estos nutrientes no fueron afectados significativamente por la variación sustancial en la calidad y cantidad del forraje. Sin embargo, estas estrategias fueron insuficientes para compensar la poca abundancia de forraje de alta calidad habitualmente presente bajo cubiertas forestales cerradas.

Nuestro modelo sobre la nutrición incluyó ecuaciones no lineales y de regresión múltiple para predecir 1) nivel dietético de ED (kcal/g forraje ingerido), basado principalmente en la abundancia de especies aceptadas ($r^2 = 0,49$ – $0,62$); y 2) nivel dietético de PD (% de forraje ingerido), basado principalmente en la abundancia de especies aceptadas, la cubierta del piso dominante y las características del lugar destinadas a indexar la humedad del suelo ($r^2 = 0,60$). También desarrollamos ecuaciones para predecir tasas de consumo por minuto que incluyen las mismas covariables, pero la varianza explicada fue ligeramente más baja (ingesta ED: $r^2 = 0,43$; ingesta PD: $r^2 = 0,45$ – $0,54$). *Con* la ayuda de estas ecuaciones, creamos perfiles de nutrición-sucesión para ilustrar la dinámica de la ingesta de ED y de PD a lo largo de toda la secuencia de sucesión para cada tipo de hábitat y área de estudio. Estos perfiles pueden ser muy útiles en la preparación de mapas espacialmente explícitos sobre los recursos nutricionales del ciervo. Dado que estos perfiles fueron desarrollados usando datos sobre la alimentación de ciervos en busca de comida, su uso debería ayudar a disminuir la incertidumbre engendrada por la utilización frecuente de variables sustitutivas como índices de recursos nutricionales.

Nuestros datos demostraron que los recursos nutricionales en los bosques del oeste de Oregón y del estado de Washington son generalmente insuficientes para las hembras de ciervo lactantes durante el verano y al empezar el otoño. Estos datos han proporcionado evidencia que la presencia de recursos nutricionales inadecuados es en gran parte responsable de la baja grasa corporal en los ciervos durante el otoño y de las reducidas tasas de gestación observadas en numerosas manadas de ciervos en el Pacífico noroeste. Nuestros datos también muestran que el valor nutricional de los hábitats es altamente variable según el contexto ecológico, las perturbaciones y las etapas de sucesión. En consecuencia, el emplazamiento de los hábitats forestales para los ciervos, la manera cómo esos hábitats son manejados y la necesidad de manejarlos pueden influenciar considerablemente el valor nutricional de un territorio. Finalmente, nuestros datos indican que existe una importante necesidad de integrar las evaluaciones nutricionales en los procesos de planificación de paisajes en donde el mantenimiento de poblaciones de ciervos abundantes y productivas es uno de los tantos objetivos de gestión forestal in el Pacífico noroeste.

Écologie Nutritionnelle du Wapiti en Été et en Automne dans le Pacifique Nord-Ouest

RÉSUMÉ Dans l'ouest des États-Unis, le wapiti (*Cervus elaphus*) est une espèce faunique d'une grande valeur socio-économique. Au niveau fédéral, il a un statut d'espèce-vedette dans la planification de l'aménagement d'un territoire. C'est pourquoi l'évaluation de l'habitat du wapiti et la planification de l'aménagement du territoire ont fait l'objet de nombreux travaux de modélisation. La mesure dans laquelle ces modèles et d'autres modèles sur l'habitat des grands ongulés tiennent compte du rôle des ressources nutritionnelles varie considérablement, probablement en raison de l'importance variable accordée par les scientifiques à l'alimentation et en raison de l'incertitude liée à la façon de mesurer et de modéliser la nutrition. Nos principaux objectifs étaient 1) de mieux comprendre comment les conditions de l'habitat influencent la dynamique de quête alimentaire et l'alimentation du wapiti en été et en automne, et 2) d'élaborer un cadre écologique pour évaluer et prédire les ressources nutritionnelles de façon à intégrer les besoins nutritionnels du wapiti dans les plans à l'échelle du paysage, dans les modèles sur les populations et dans les modèles sur l'évaluation de l'habitat. Nous avons suivi la quête alimentaire du wapiti et évalué la réponse de ce dernier aux activités de récolte du bois par coupe à blanc et aux activités d'éclaircies commerciales, aux successions forestières et aux saisons dans un ensemble de sites ayant un potentiel écologique. Nous avons également déterminé dans quelle mesure les communautés végétales comblaient les besoins nutritionnels des femelles en lactation et des faons. Nous avons réalisé notre étude dans les forêts ombrophiles tempérées du Pacifique Nord-Ouest sur des terres forestières publiques et industrielles.

Nous avons évalué les relations entre les conditions de l'habitat et l'alimentation du wapiti dans des communautés végétales pour différentes tranches d'âge de peuplement et différentes conditions écologiques dans 3 territoires, soit 1 près de la frontière canadienne dans le nord des monts Cascades (Nooksack), 1 dans la chaîne côtière au sud-ouest d'Olympia, Washington (Willapa Hills) et 1 dans la région centrale des monts Cascades près de Springfield, Oregon (Springfield), entre la fin du mois de juin 2000 et le mois de novembre 2002. Dans 98 à 143 macroparcelles par territoire étudié, nous avons mesuré l'abondance du fourrage par espèce végétale, l'énergie digestible par groupe biologique de végétaux et l'étage dominant de la forêt. Dans un sous-ensemble de ces macroparcelles (~30 par territoire étudié), nous avons gardé 4 femelles apprivoisées qui étaient en lactation ainsi que leurs faons dans des enclos électrifiés ($n = 15\text{--}25$ adultes par année) et nous avons mesuré les budgets d'activité, la composition de l'alimentation, le choix du fourrage et d'autres paramètres associés à la quête alimentaire, les taux d'énergie digestible (ED; kcal/g), le pourcentage de protéine digestible (PD; %) du fourrage ingéré ainsi que le taux d'ingestion d'ED et de PD. Dans chaque territoire étudié, nous avons gardé les wapitis dans 5 de ces enclos pendant une période de temps plus longue (13 à 21 jours) afin de suivre de près les changements dans les réserves lipidiques des adultes et l'évolution de la croissance des faons. Nous avons développé des équations pour prédire l'ED et le PD et le taux d'ingestion à la minute de chacun et avons intégré ces équations dans un modèle prédictif sur la nutrition qui tient compte des attributs de la végétation et des influences écologiques du site.

L'abondance totale du fourrage dans l'écozone de la pruche de l'Ouest après la récolte du bois par coupe à blanc effectuée à faible altitude ou à altitude moyenne ($\leq 1\,000$ m) variait entre un maximum de 3 000 à 4 500 kg/ha dans des peuplements de 5 à 10 ans et 100 à 300 kg/ha dans des peuplements de 20 à 50 ans avec seulement des augmentations modérées jusqu'au dernier stade de succession. Les profils étaient similaires dans des forêts de plus haute altitude (1 000 à 1 800 m) bien que les pics et les creux dans l'abondance du fourrage se développaient plus lentement. Les arbustes à feuilles caduques, les herbacées et les graminées étaient abondants dans les forêts aux premiers stades de succession écologique après une perturbation, mais étaient rapidement remplacés par des arbustes à feuillage persistant et des fougères tolérant l'ombre à mesure que le couvert coniférien se fermait 15 à 20 ans plus tard dans les zones forestières de faible altitude et 20 à 40 ans plus tard dans les zones de haute altitude. L'énergie

digestible dans les groupes biologiques de végétaux diminuait généralement en fonction des saisons et de l'évolution de la succession, augmentait avec l'altitude et était la plus élevée dans les herbacées et dans les arbustes à feuilles caduques et la plus faible dans les arbustes à feuillage persistant et dans les fougères tolérant l'ombre.

L'étude a révélé une étroite relation asymptotique entre les taux d'ED dans l'alimentation du wapiti et l'abondance (kg/ha) des espèces végétales qui étaient ingérées en proportions égales ou supérieures à leur disponibilité (c.-à-d. les espèces acceptées). Des diminutions marquées de l'ED sont survenues dans des peuplements contenant <400 kg/ha à 500 kg/ha d'espèces acceptées, surtout parce que les wapitis avaient commencé à consommer davantage d'espèces évitées. Le profil asymptotique était généralement le même quelle que soit la saison, le territoire étudié et le type d'habitat (catégories de végétation naturelle potentielle) bien que l'asymptote était en moyenne de 10 à 12% supérieure dans les forêts de haute altitude *vs* les forêts de faible altitude. Les espèces acceptées dans les premiers stades de succession écologique étaient en moyenne 7 à 10 fois plus abondantes que dans les stades intermédiaires et les derniers stades de succession, et les taux d'ED variaient en conséquence. Les éclaircies avaient peu d'influence sur l'ED dans les peuplements de 20 à 60 ans. Quant aux pourcentages de PD, ils n'étaient pas reliés à la composition du fourrage ni à l'abondance des espèces acceptées ou évitées et variaient peu entre les forêts de faible altitude et les forêts de haute altitude. Le pourcentage de PD augmentait avec l'augmentation de la couverture de l'étagé dominant, était plus élevé dans les peuplements éclaircis et les peuplements de feuillus (particulièrement les peuplements de feuillus dont le sol était saturé à la fin de l'été), diminuait en fonction des saisons et était le plus bas dans les communautés forestières les plus arides de notre étude. Globalement, la majorité des variations dans les pourcentages de PD était attribuable aux conditions d'humidité du sol et aux saisons.

Les relations entre l'apport en nutriments et les conditions de la végétation variaient selon le territoire étudié et le type d'habitat. Néanmoins, les wapitis maintenaient un taux d'ingestion d'ED qui était environ deux fois plus élevé dans les forêts aux premiers stades de succession que dans les forêts à couvert fermé. Les taux d'ingestion de PD étaient similaires dans les forêts aux premiers stades de succession et dans les forêts à couvert fermé, même s'il y avait légèrement moins de PD dans les premiers stades de succession. L'apport en protéines était plus élevé dans les peuplements éclaircis et dans les peuplements riverains de feuillus. Dans les premiers stades de succession, les taux d'ED correspondaient généralement au taux de 2,7 kcal/g de fourrage ingéré (taux nécessaire pour maintenir les réserves lipidiques des femelles en lactation en été) dans les forêts de faible altitude et dépassaient cette valeur dans les forêts de haute altitude. Dans les forêts à couvert fermé, les taux d'ED étaient en moyenne inférieurs au taux nécessaire pour combler les besoins du wapiti – taux sensiblement inférieurs (2,25 à 2,5 kcal/g) dans les forêts de faible altitude et légèrement inférieurs (2,4 à 2,65 kcal/g) dans les forêts de haute altitude. Le taux d'ingestion d'ED était le paramètre où les déficiences étaient les plus marquées; ce taux correspondait en moyenne à 50% des besoins (28 kcal/min; 21 000 kcal/jour) dans les forêts à couvert fermé et à 80% des besoins dans les forêts aux premiers stades de succession. Par contre, les pourcentages de PD et les taux d'ingestion de la PD correspondaient généralement aux besoins estimés ou les dépassaient (PD 6,8%; 380 g/jour) dans de nombreux types d'habitat échantillonnés. Les forêts relativement arides situées à faible altitude constituaient les habitats les plus susceptibles de présenter des déficiences dans le taux d'ingestion de la PD.

La dynamique des réserves lipidiques et la croissance des faons ont confirmé les déficiences nutritionnelles mises en évidence par nos données sur les taux d'ED. Les réserves lipidiques des wapitis adultes ont diminué au cours de tous les essais à des taux qui correspondaient généralement à ce que nous nous attendions compte tenu des taux d'ED consommés par les wapitis. Le taux de variation des réserves lipidiques était inversement proportionnel à l'abondance des espèces acceptées. Les faons ont grandi à un rythme d'environ la moitié de ce dont ils sont capables (1 kg/jour) lorsque leur apport estival en nutriments est suffisant. La croissance quotidienne des faons était directement liée à l'ED et aux protéines ingérées par leur mère.

Les wapitis ont suppléé aux options de fourrage limitées dans de nombreuses communautés végétales en adoptant plusieurs stratégies comportementales. En général, leur choix ont porté surtout sur des plantes ayant un taux d'ED plus élevé. Ces espèces choisies ont fait partie de leur alimentation 5 fois plus souvent que les espèces évitées, bien que les espèces évitées soient 10 fois plus abondantes. Lorsque l'abondance des espèces acceptées a diminué et atteint environ 400 kg/ha, les wapitis ont commencé à ingérer davantage d'espèces évitées. Cette stratégie a retardé la diminution du taux d'ingestion de fourrage par minute et la diminution du taux d'ingestion d'ED tant et aussi longtemps que l'abondance des espèces acceptées est demeurée au-dessus d'environ 200 kg/ha, malgré une diminution du taux d'ED devenue apparente lorsque l'abondance des espèces acceptées a atteint <400 kg/ha à 500 kg/ha. Les wapitis se sont déplacés plus rapidement pendant leur quête alimentaire afin de pallier la très faible abondance de fourrage total dans certaines communautés végétales, ont augmenté la fréquence des bouchées à mesure que diminuait la masse des bouchées, ont passé plus de temps à se nourrir la nuit dans les enclos où le fourrage total était peu abondant ou les taux d'ED étaient relativement faibles, et ont augmenté la durée de rumination, en particulier à mesure qu'ils consommaient davantage de fibres alimentaires. Les taux d'ED, le pourcentage de PD et le taux d'ingestion de ces nutriments étaient par conséquent insensibles aux énormes variations dans la qualité et la quantité globales du fourrage. Néanmoins, ces stratégies étaient

insuffisantes pour pallier la faible abondance de fourrage de haute qualité habituellement présent sous la couverture des forêts fermées.

Notre modèle sur la nutrition incluait des équations non linéaires et de multiples équations de régression destinées à prédire 1) le taux d'ED (kcal/g de fourrage ingéré) en se basant principalement sur l'abondance des espèces acceptées ($r^2 = 0,49\text{--}0,62$) et 2) le pourcentage de PD (% de fourrage ingéré) en se basant principalement sur l'abondance des espèces acceptées, sur la couverture de l'étage dominant et sur les caractéristiques du site pour déterminer l'indice d'humidité du sol ($r^2 = 0,60$). Des équations additionnelles destinées à prédire les taux d'ingestion par minute incluaient les mêmes covariables, mais la variance expliquée était légèrement plus faible (ingestion d'ED: $r^2 = 0,43$; ingestion de PD: $r^2 = 0,45\text{--}0,54$). À l'aide de ces équations, nous avons créé des profils de nutrition-succession pour illustrer la dynamique de l'ingestion d'ED et de PD dans toute la séquence évolutive des peuplements, et ce, pour chaque type d'habitat et de territoire étudié. Ces profils pourront servir d'intrants pour élaborer des cartes spatiales explicites sur les ressources nutritionnelles du wapiti. Puisque l'élaboration de ces cartes a fait appel à des données sur l'alimentation de wapitis en quête de nourriture, elles devraient réduire une bonne part de l'incertitude engendrée par les variables de remplacement qui sont souvent utilisées comme indicateurs de ressources nutritionnelles.

Nos données montrent que les ressources nutritionnelles des forêts de l'ouest de l'Oregon et de l'état de Washington sont généralement insuffisantes pour les wapitis en lactation en été et tôt à l'automne. Ces données ont montré que des ressources nutritionnelles inadéquates sont en grande partie responsables des faibles réserves lipidiques du wapiti à l'automne et des taux réduits de gestation observés chez de nombreuses hardes de wapitis dans le Pacifique Nord-Ouest. Nos données montrent également que la valeur nutritionnelle des habitats est très variable selon le contexte écologique, les perturbations et les stades de succession. Par conséquent, les habitats à aménager, la façon de les aménager et la nécessité de les aménager peuvent influencer considérablement la valeur nutritionnelle d'un territoire. Finalement, nos données indiquent qu'il existe un important besoin d'intégrer les évaluations nutritionnelles dans les processus de planification des paysages, car la préservation d'abondantes populations productives de wapitis est l'un des objectifs d'aménagement des forêts de la région du Pacifique Nord-Ouest.

Contents

INTRODUCTION	7	<i>Foraging dynamics</i>	26
STUDY AREA	11	<i>Nutrient content in elk diets</i>	31
METHODS	12	<i>Intake rates</i>	34
Vegetation Sampling	14	Foraging Experiments: Body Fat and Calf Growth	37
Forest Succession Patterns	15	Nutrition Models	38
Overstory and understory development	15	DISCUSSION	43
Forage quality development	15	Mechanisms Linking Plant Communities and Foraging Responses	44
Foraging Experiments	16	Forest management and succession	44
General field procedures	16	Foraging behavior	47
Dietary composition and selection	17	Nutritional responses	53
Foraging dynamics	17	Summer Nutritional Limitations for Wild Elk Herds	56
Foraging Experiments: Body Fat and Calf Growth	19	Nutrition in Habitat Evaluation and Landscape Planning	61
Nutrition Models	19	MANAGEMENT IMPLICATIONS	62
RESULTS	20	Habitat Evaluation and Planning	62
Forest Successional Patterns	20	Habitat Management	63
Overstory development	20	SUMMARY	64
Understory development	21	ACKNOWLEDGMENTS	65
Forage quality development	24	LITERATURE CITED	65
Foraging Experiments	25	APPENDICES	71
Dietary composition and selection	25		

INTRODUCTION

Identifying and forecasting responses of animal populations to habitat attributes, climate, and disturbance regimes remain among the most basic goals of applied and theoretical ecology. Nevertheless, understanding responses of animal populations to their environment is a daunting challenge that “remains a

surprisingly contentious issue” (Schmitt and Holbrook 2007). The state of knowledge linking ungulate populations with their environment provides perhaps one of the best examples of the difficulty. Although ungulates are among the most studied wildlife on the planet, a stringently validated approach still does not exist for linking environment and populations that is useful for habitat management and landscape planning.

Declines in large ungulate populations including bighorn sheep (*Ovis canadensis*; Wakelyn 1987), caribou (*Rangifer tarandus*; Festa-Bianchet et al. 2011), mule deer (*Odocoileus hemionus*; Carpenter 1998), moose (*Alces alces*; Murray et al. 2006, Monteith et al. 2015), and elk (*Cervus elaphus*; Johnson et al. 2005, White et al. 2010) highlight the need for clarifying influences of habitat characteristics on ungulate populations.

Many environmental factors influence dynamics of ungulate populations, but the importance of nutrition as a driver of reproduction, health, and resilience to harsh weather is well-supported, based particularly upon controlled studies of livestock (National Research Council 1984, 1985). Controlled studies for elk similarly illustrated that inadequate nutrition influences a host of performance variables such as juvenile growth, pregnancy probability, fat accretion rates, overwinter survival probability, sexual maturity, and timing of breeding (Cook et al. 1996, 2004). Most of these performance responses reflected nutrition during summer and early autumn and were sensitive to relatively small variation in digestible energy (DE) content of food, a type of multiplier effect (White 1983). Parker et al. (1999) noted that nutrient requirements, foraging and digestive efficiencies, and forage characteristics provide quantifiable cause-and-effect relations that influence nutritional condition, growth, reproduction, and survival. They argued that nutritional ecology offers a quantitative basis for scaling up key relations between individual animals and their habitats to populations across landscapes.

Nevertheless, unknowns regarding the influence of nutrition undoubtedly hamper applications for management purposes, including 1) extent of reductions in performance of individual animals and productivity of populations as a function of nutritional limitations across space and time; 2) the seasonality of nutritional influences, across-season carry-over effects, and stochastic influences of variable weather and other abiotic factors; 3) attributes of environment and vegetation communities that explicitly account for nutritional limitations where they occur; and 4) density-dependent and -independent effects that may alter the magnitude of nutritional influences (Cook 2002). A contributing problem is that identifying nutrition levels (e.g., nutrient content of diets, intake rate of nutrients), nutritional condition (as defined by Harder and Kirkpatrick [1994]; e.g., body fat), and other performance responses; understanding interactions between foraging behavior and vegetation attributes on nutrition and performance; and translating these relationships to populations is difficult for highly mobile ungulates in complex and dynamic environments. Studies of nutritional influences for most ecological settings in North America do not exist, leaving management biologists with little local knowledge of influences of nutritional resources.

The consequences of the lack of relevant nutritional information for management is particularly well-illustrated for elk in the western United States. A large number of habitat evaluation models developed for elk (Leege 1984, Lyon et al. 1985, Wisdom et al. 1986, Thomas et al. 1988) either ignored nutrition or accounted for nutrition in ways that were never validated and were possibly ineffective (Edge et al. 1990, Roloff et al. 2001, Cook et al. 2004). Hence, one of the most important pathways through which habitat may influence productivity of elk populations was excluded from extant habitat evaluation and

planning tools, or was never used for management and planning purposes (Roloff et al. 2001). Because elk were considered a featured species on many public lands of the region, and because many of the habitat models were explicitly used for forest planning (Thomas 1982, Christensen et al. 1993), these models had and continue to have substantial implications for land management on behalf of elk on public lands in the western United States.

Linking ungulate population dynamics to vegetation, other environmental attributes, and changes in these attributes over time involves accounting for a number of dynamic interactions between animals and their environment (Fig. 1). Nutritional levels that herbivores can acquire at fine scales are a function of vegetation attributes, but the specific levels of dietary quality and intake rate of nutrients may be strongly influenced by dynamic foraging behavior of herbivores, such that nutrition may be significantly different than if they simply foraged at random (Illius 1997, Searle et al. 2007). Via selection of plant species and plant parts and corresponding bite size, herbivores may affect levels of nutrients and toxic compounds in their diets, and thus intake rates of forage and nutrients. They may further alter daily intake of nutrients by adjusting intensity of foraging (bite rate) and time each day spent foraging. Important tradeoffs exist between locating and consuming forage of high quality versus consuming forage rapidly enough to satisfy total daily nutrient requirements (Bailey et al. 1996). Across heterogeneous landscapes, herbivores may select plant communities that provide relatively high nutrition per amount of foraging effort to enhance nutritional status. Foraging behavior at fine scales and habitat selection at medium scales are potentially powerful mechanisms by which herbivores may enhance their nutrition, particularly in nutritionally depauperate environments (Hobbs 2003, Searle et al. 2007). As such, standard forage quantity or even forage quality surveys designed to describe nutritional resources available to populations of herbivores may poorly reflect actual levels of nutrition that herbivores acquire. Various proxy variables presumed to index nutritional resources also may be markedly inadequate (e.g., forest stand age, total forage production; Searle et al. 2007).

We contend that important advances in the realm of nutritional ecology ultimately require integrating at least 3 approaches: 1) top-down evaluations using nutritional condition, pregnancy rates, and other performance measures to provide insights of nutritional adequacy at large scales; 2) bottom-up evaluations at fine scales regarding interactions (i.e., mechanisms) between foraging behavior and vegetation attributes on nutritional responses; and 3) habitat-use evaluations that describe selection among nutritional resources and other habitat attributes. The assessment of nutritional condition, primarily using ultrasonography and body condition scores (Stephenson et al. 1998, 2002; Cook et al. 2001, 2010), supplemented with estimates of pregnancy rates and body mass (Cook et al. 2013), has progressed in recent years. These measures are providing valuable new insights regarding influences of nutrition on large ungulates in North America (Gerhart et al. 1997, Keech et al. 2000, Cook et al. 2013, Monteith et al. 2015). Levels of nutritional condition result from the separate effects of nutritional value of the environment with the nutrient demands of the animal (Parker

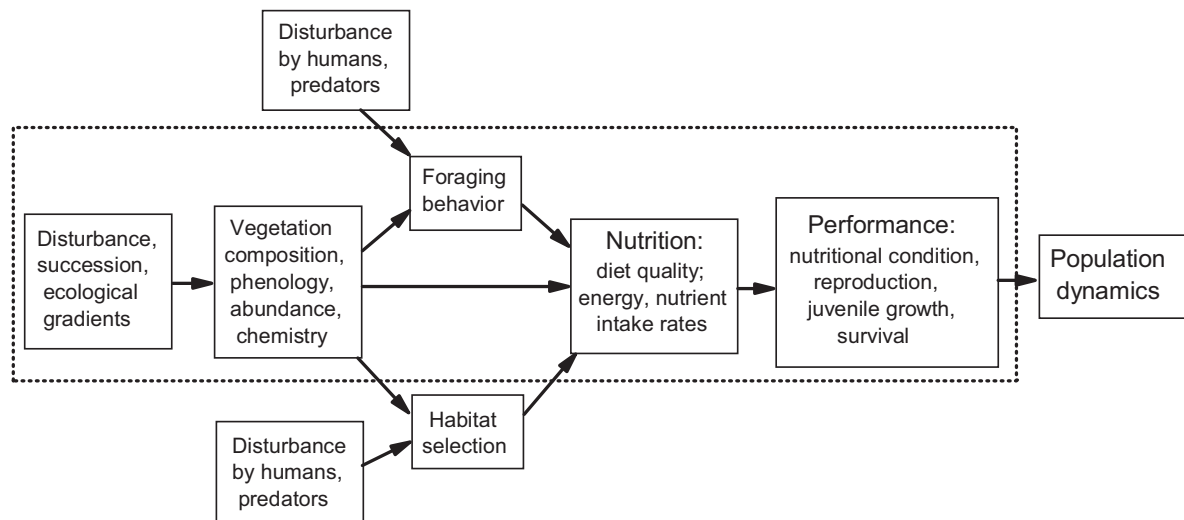


Figure 1. Conceptual illustration of habitat influences on animal performance and population dynamics operating primarily through nutritional pathways (herbivore-forage feedbacks, winter weather, and direct effects of predation and hunting on population dynamics are excluded for simplicity). Nutrition is a direct result of interactions between 1) forage quality and quantity and foraging behavior within plant communities; and 2) distribution of vegetation communities and habitat selection among communities, each of which may be influenced by disturbance from humans and predators. We focused on identifying relationships between vegetation and elk foraging behavior and nutrition, and nutrition and performance in homogeneous stands of forestland habitats (dotted rectangle).

et al. 2009) and can strongly affect fitness and performance (Harder and Kirkpatrick 1994). Thus, estimates of nutritional condition are valuable measures. However, they typically cannot identify causes of observed levels of condition. Animals may be thin because of inadequate nutrition, increased daily movements due to disturbance by human activities (Davidson et al. 2012) and predators (Creel et al. 2007), or because fear and displacement disrupt normal feeding patterns or force use of habitats that offer poor nutrition (Creel et al. 2007, but see White et al. 2011, Middleton et al. 2013b). Further, it is not clear the extent to which performance responses are a result of classic density-dependent mechanisms or are due to density-independent ecological and successional influences on abundance, chemistry, and species composition in plant communities (DeYoung et al. 2008, Cook et al. 2013). Even in situations where relatively low nutritional condition is directly due to inadequate nutrition, estimates of nutritional condition alone cannot identify what aspects of vegetation are responsible. Thus, information at fine scales is essential to fully account for observed patterns of animal performance and habitat use at broad scales. This issue is not trivial; lacking reliable knowledge of mechanistic links between vegetation, nutrition, nutritional condition, and ultimately productivity precludes development of reliable nutrition-explicit habitat evaluation models and effective habitat management strategies.

Herds of Rocky Mountain (*C. e. nelsoni*) and Roosevelt elk (*C. e. roosevelti*) offer considerable value for the public in the temperate rainforests in western Oregon and Washington, USA. These forests are among the most productive in the world, with high annual precipitation and moderate ambient temperatures that vary with elevation and latitude (Franklin and Dyrness 1988). Despite productive plant communities, suspicions exist that many elk herds in the region experience important nutritional deficiencies that affect condition, reproduction, and population trends (Ferry et al. 2001, Bender et al. 2006,

Washington Department of Fish and Wildlife 2006). For example, early studies demonstrated relatively low levels of body fat in autumn and very low (<50%) to moderately reduced pregnancy rates (<80%; Trainer 1971, Kuttel 1975, Smith 1980, Harper 1987, Stussy 1993).

Recent surveys of 12 elk herds in the region illustrated low nutritional condition and pregnancy rates that were attributed to habitat conditions on summer range but also demonstrated marked variation in autumn body fat and pregnancy among herds due to reasons not yet fully identified (Cook et al. 2013). Positive population responses of elk after the 1980 eruption of the Mount St. Helens volcano in western Washington signaled that disturbance and succession, likely operating through nutritional pathways, may greatly influence dynamics of large ungulate populations in forested ecosystems (Merrill 1987). Similar responses have been reported elsewhere (Pengelly 1963; Irwin and Peek 1983; Gill et al. 1996; Riggs et al. 1996; Bomar 2000; Peek et al. 2001, 2002). Forest overstory removal following natural disturbance or regeneration logging—the dominant silvicultural practice—shifts understory vegetation composition from shade-tolerant to shade-intolerant shrubs and herbs, and elevates production 2- to 5-fold within 2 to 4 years after disturbance (Alaback 1982, Franklin and Dyrness 1988, Jenkins and Starkey 1996). Additionally, Cook et al. (2013) identified north-south and east-west gradients in nutritional condition and pregnancy rates of elk in the region that may reflect climatological and edaphic gradients in vegetation composition, phenology, and productivity.

The successional influences on forage quantity suggest that the nutritional value (i.e., dietary DE, digestible protein [DP] and intake rates of these relative to requirement of the animal) of plant communities may be relatively high in early seral stages and wane as forest succession advances (Hett et al. 1978, Jenkins and Starkey 1996). However, forage quality more than forage quantity may influence nutritional value of vegetation

communities to ungulates in the Pacific Northwest (Hanley et al. 1987). Plants in early seral stages may have greater tannin astringency and phenolics, and contain lower levels of nitrogen, phosphorus, potassium, and digestible protein than those in late seral forests (Hanley et al. 1987, Van Horne et al. 1988, Happe et al. 1990). Low-light levels under dense forest canopies that reduce photosynthesis, carbon-fixation, and lignification evidently were responsible for greater concentrations of nitrogen, phosphorus, and potassium, and lower tannins accounted for ≤ 2 -fold greater digestibility of protein in plants under forest canopies (Hanley et al. 1987, Van Horne et al. 1988).

This body of research questioned the assumption that high forage quantity in early seral stages provided greater nutritional value than late seral stages. However, the studies relied on paired comparisons of nutrient levels in selected plant species in early seral stages versus those in closed-canopy forests and thus 1) may have incompletely accounted for the ability of ungulates to choose plant species and parts to enhance nutrition; and 2) did not consider that highly lignified, low-quality plants (ferns, conifers, and some shrubs) often dominate in late seral stages in forests of western Oregon and Washington (Merrill 1994). For example, in early seral stages created by the eruption of Mount St. Helens, elk consumed more early seral forbs and graminoids, diets were significantly greater in DE than in older forests, and protein levels were similar among the 2 seral stages (Merrill et al. 1995). Hence, the relative and absolute abundance of palatable, nutritious forage versus unpalatable forage of low quality may play an important role in nutritional ecology of elk. Much remained to be learned about the relationship of elk nutrition with vegetation, disturbance, and succession in the region.

We used captive, highly tractable elk to sample foraging dynamics and nutrition during summer in plant communities of the Pacific Northwest at 3 study areas, the Nooksack area in the northern Cascades of northwestern Washington, the Willapa Hills in the coastal foothills of southwestern Washington, and the central Cascades of western Oregon near Springfield, Oregon. We deployed adult females with calves in temporary enclosures constructed in native vegetation communities spanning a wide range of seral stages and ecological site potentials. Our over-arching goal was to develop greater understanding of how habitat conditions, particularly with respect to forest management, influenced foraging dynamics and nutrition of elk in summer and autumn. We designed our study to provide results to facilitate landscape planning, habitat evaluation and management, and research. Hauffer (1994) noted landscape planning for wildlife tends to be based on classification of overstory vegetation types with little regard to succession, and indicated that this approach often ignores underlying ecological influences and is inadequate for predicting future conditions. We linked our nutritional data to disturbance regime, succession, and ecological site potentials to enhance their value for landscape planning and management.

We focused our research on ranges occupied during summer and autumn, because important life processes at this time (late gestation, lactation, juvenile growth, breeding, accretion of endogenous energy) impose the greatest nutritional demands of the annual cycle (Ofstedal 1985; Haigh and Hudson 1993; Cook et al. 1996, 2004; Parker et al. 1999). Global evidence is

increasing that nutrition in summer and early autumn often fails to satisfy nutritional requirements for these processes in many temperate ecosystems, leading to important depressing effects on productivity of ungulate herds (Cr te and Huot 1993, Hjeljord and Histol 1999, Dale et al. 2008, Cook et al. 2013: 6, Hurley et al. 2014). Such depressing effects also are suspected to occur in the temperate rainforests in the Pacific Northwest United States (Trainer 1971, Harper 1987, Cook et al. 2013).

Our specific objectives included the following:

1. To quantify linkages between understory vegetation and other site characteristics with a) foraging dynamics of lactating elk (e.g., DE and DP levels in consumed foods, nutrient intake rates, and overall forage intake rates); and b) changes in nutritional condition of these females and growth of their calves.
2. To improve understanding of how forest management influences foraging behavior and nutrition of elk and likely affects the nutritional value of landscapes in summer and autumn.
3. To develop an ecological-successional framework for predicting nutrition across landscapes that might form a basis for landscape-scale mapping and modeling of these resources.
4. To evaluate potential for fine-scale vegetation attributes to be a primary cause of inadequate nutrition long suspected in the region (Trainer 1971, Harper 1987, Cook et al. 2013).
5. To explicitly identify what aspects of vegetation communities may account for inadequate nutrition.

Nutrition is a function of interactions between foraging behavior (plant selection, bite mass and rate, speed while foraging, time spent feeding and ruminating each day) and abundance, nutrient content, and composition of plant species in vegetation communities. In this context, we evaluated the following hypotheses. First, elk are unable to acquire levels of nutrition (i.e., DE and DP content of elk diets and intake rates [i.e., per min, per day] of these nutrients) in many vegetation communities and seral stages common on our study areas that satisfy requirements for lactating females in summer and growth of their calves during summer and early autumn. Support for this hypothesis would suggest that relatively low levels of nutritional condition, pregnancy rates, and other measures of performance reported in some areas of our study region are likely due to inadequate nutrition. Second, plant community characteristics and levels of nutrition that elk acquire in native plant communities significantly influence body fat dynamics of adults and growth of their calves. To a large degree, identification of nutritional value of plant communities must rely on comparisons of observed levels of nutrition to estimates of published nutritional requirements for elk (e.g., Cook et al. 2004). Testing this hypothesis will help evaluate the extent to which relations between vegetation and nutrition translate to relations between vegetation and animal performance. Finally, nutrition of elk varies significantly in response to ecological site conditions and forest succession patterns largely due to changes in understory vegetation composition and abundance. If true, then the spatial and temporal distribution of nutrition across landscapes can be identified and predicted, and thereby incorporated into landscape

planning and habitat management protocol that address current conditions and habitat changes across landscapes in the future.

STUDY AREA

We conducted field work between the Pacific Ocean and the Crest of the Cascades (Fig. 2) in 3 separate physiographic provinces within the broader rainforest ecosystem: Nooksack (2002) in the Northern Cascades, Springfield (2000–2001) in the Western Cascades, and Willapa Hills (2001) in the Coast Ranges provinces (Franklin and Dyrness 1988). Annual precipitation

declined and ambient temperature increased from north-to-south in the Cascades, with drier and warmer conditions at Springfield than at Nooksack. In contrast, Willapa Hills had milder winter temperatures and higher annual precipitation due to greater maritime influences near the ocean. Soils were largely derived from sandstones and mudstones in the Coast Range and basalt from volcanoes in the central Cascades near Springfield, the latter of which transitioned to granite in the northern Cascades near Canada (Pojar and MacKinnin 1994).

We selected our 3 study areas to be representative of the temperate rainforests of western Oregon and Washington and to encompass differences in biogeoclimatic conditions that existed among the 3 physiographic provinces. We collected data primarily on private and state forestlands, largely because road closures provided security for workers and elk. Those lands also provided a greater variety of silvicultural treatments and successional stages than adjacent federal lands. Other selection criteria included availability of large contiguous blocks generally under single ownership and availability of extensive information on stand-level management history.

The 250-km² Nooksack study area (122° 0' W, 48° 35' N) was located in the northern Cascades Mountains south of Mt. Baker, Washington along the South Fork of the Nooksack River. Land use at Nooksack was primarily industrial tree farm and ownership was Crown Pacific Timber Company and the Washington Department of Natural Resources, although areas along the Skagit River on the southern periphery of the study area were used for hay production. Topography was generally steep and mountainous in the north to rolling foothills in the south with elevations ranging from 100–1,400 m. Total precipitation ranged from 120–300 cm annually depending on elevation (Franklin and Dyrness 1988). Cumulative precipitation and mean minimum temperature in January was 502 mm and –1.3°C. Cumulative precipitation in July averaged 33 mm, with a temperature range of 10.4°C (minimum) to 23.7°C (maximum; Daly et al. 1994).

The 300-km² Willapa Hills study area (123° 10' W, 46° 30' N) was located 80 km southwest of Olympia, Washington along the Chehalis River and South Fork Chehalis River. Land use at Willapa Hills was primarily industrial tree farm owned mostly by Weyerhaeuser Company. Topography included rolling foothills and steep narrow creek and river valleys with elevations ranging from 100–900 m. Annual precipitation varied from 150–250 cm depending on elevation (Franklin and Dyrness 1988). Cumulative precipitation and mean minimum temperature in January was 388 mm and 2.6°C. Cumulative precipitation and temperature range in July were 23 mm and 10.7°C (minimum) to 22.9°C (maximum; Daly et al. 1994).

The 250-km² Springfield study area (122° 45' W, 44° 13' N) was located 25 km northeast of Springfield, Oregon between the McKenzie River to the south and the Mohawk River to the north. We collected supplemental vegetation data in old forests at the H. J. Andrews Experimental Forest located 15 km east of the Springfield study area. Land use at Springfield was primarily industrial tree farm that was owned mostly by Weyerhaeuser Company. The Experimental Forest was used for a variety of forest ecology studies and was a Biosphere Reserve in United Nations Educational, Scientific and Cultural Organization's (UNESCO) Man and the Biosphere program. Topography was

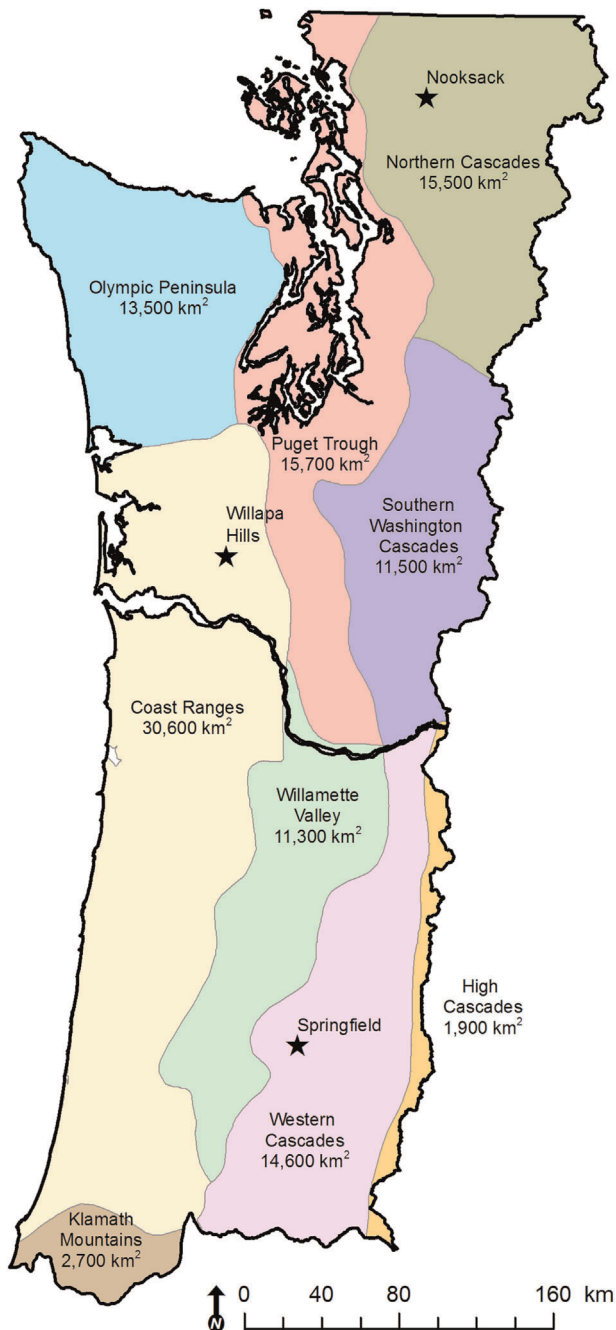


Figure 2. Location of the Nooksack, Willapa Hills, and Springfield study areas in Oregon and Washington, USA. The western boundary of the region coincides with the crest of the Cascades Mountain Range. Ecological provinces are from Franklin and Dyrness (1988).

generally rolling but with occasional steep slopes ranging from 200–1,400 m. Annual precipitation ranged from 100–175 cm, and cumulative precipitation and mean minimum temperature in January was 289 mm and 0.7°C. Cumulative precipitation and temperature in July were 9 mm and 8.8°C (minimum) to 26.0°C (maximum; Daly et al. 1994).

Three primary forest zones occurred across the 3 study areas: the western hemlock (*Tsuga heterophylla*) forest series (WHS) predominated (common abbreviations used in the text are presented in Table 1) at lower elevations (as high as 1,000 m at southern latitudes). Western hemlock and Douglas fir (*Pseudotsuga menziesii*) usually dominated in this series, with the latter more common on drier and in younger stands. Western red cedar (*Thuja plicata*) and several species of hardwoods including red alder (*Alnus rubra*) and maple (*Acer* spp.) also occurred sporadically. Understories varied with site conditions. Salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*) typically dominated under forest canopies on drier sites with swordfern (*Polystichum munitum*) and salmonberry (*Rubus spectabilis*) dominant on wetter sites. Understory plant communities following stand-replacing disturbance were more diverse, and included a variety of shade-intolerant or semi-tolerant species including snowberry (*Symphoricarpos* spp.), thimbleberry (*Rubus parviflorus*), red alder, maple, blackberry (*Rubus* spp.), bracken fern (*Pteridium aquilinum*), thistle (*Cirsium* spp.), fireweed (*Epilobium angustifolium*), cat's-ear (*Hypochaeris radicata*), and velvet grass (*Holcus lanatus*; Franklin and Dyrness 1988, Henderson et al. 1992).

At mid-elevations, forests transitioned into the Pacific silver fir (*Abies amabilis*) forest series (PSS). Western hemlock typically co-dominated with Pacific silver fir, and Douglas fir, western red cedar, and several species of hardwoods (alders and maples) were common. Lady-fern (*Athyrium filix-femina*), huckleberry (*Vaccinium* spp.), salmonberry, twinflower (*Linnaea borealis*), and trailing blackberry (*Rubus ursinus*) were common in the under-stories. In early seral stands, many of these taxa were well represented along with a variety of shade-intolerant and semi-tolerant taxa, including red alder, elderberry (*Sambucus* spp.), fireweed, bracken fern, and trailing blackberry (Franklin and Dyrness 1988, Henderson et al. 1992).

Table 1. List of common abbreviations used in text.

Abbreviations	Definition
AccSpp	Abundance of accepted plant species (kg/ha) (NeuSpp + SelSpp)
AvdSpp	Abundance of avoided plant species (kg/ha)
AllSpp	Abundance of all understory plant species (kg/ha)
BSA	Bovine serum albumin precipitation (mg precipitate/mg foliage)
DE	Digestible energy (kcal/g)
DE-GFS	Mean DE content of graminoids, forbs, and deciduous shrubs combined
DP	Digestible protein (% of dry matter)
MHS	Mountain hemlock series habitat type
NeuSpp	Abundance of neutral plant species (kg/ha)
PSS	Pacific silver fir series habitat type
SelSpp	Abundance of selected plant species (kg/ha)
WHS-salal	Western hemlock series-salal habitat type
WHS-swordfern	Western hemlock series-swordfern habitat type

The mountain hemlock (*Tsuga mertensiana*) series (MHS) occurred at high elevations (as low as 600 m at northern latitudes) between the PSS and alpine communities and was the wettest and coolest forest zone on our study areas. Pacific silver fir and mountain hemlock usually co-dominated, with western hemlock, subalpine fir (*Abies lasiocarpa*), and western red cedar often present. Common shrubs included huckleberry, white-flowered rhododendron (*Rhododendron albicaulis*), false huckleberry (*Menziesia ferruginea*), and mountain-ash (*Sorbus sitchensis*), and forbs included deer fern (*Blechnum spicant*), bunchberry (*Cornus canadensis*), and five-leaved bramble (*Rubus pedatus*). Early seral communities that may persist for decades tended to support similar species in varying amounts (Franklin and Dyrness 1988).

Forest management was relatively intensive on the private and state-owned timberlands on all our study areas, particularly in the WHS and PSS. Clearcutting was the common logging approach with stand rotations ranging from 40–60 years; logged stands were slash piled and usually burned. Foresters typically applied herbicide treatment just after logging to reduce the residual underbrush, planted conifer seedlings, and sometimes used a second herbicide treatment to enhance early growth of planted conifers. This process was usually required ≤ 2 years after logging, an intensive program that reflected requirements of state reforestation regulations. Precommercial thinning was evident in a few early seral stands that we sampled to reduce competition from several species of hardwood trees, mainly red alder. Commercial thinning also was occasionally applied on our study areas.

Elk were the Roosevelt subspecies at Willapa Hills and the Rocky Mountain subspecies at Nooksack and Springfield (Cook et al. 2013). The elk population at Nooksack was estimated at about 300 over 1,230 km², about 0.25 elk/km² (Davison 2002), and was not hunted because of low population numbers. However, mark-resighting surveys in 2006 indicated that twice this many elk were present (McCorquodale et al. 2012; included an introduction of 98 elk between 2002 and 2006), suggesting densities were probably 20% to 50% higher (~ 0.35 elk/km²) at the time of our study (2002). Elk were hunted at the other 2 study areas, and local density was largely unknown. Based on anecdotal observations (number of groups with radio-collared elk and group size; Cook et al. 2013) during 4 helicopter capture operations on our Springfield study area, at least 75 elk and as many as 125 elk probably were present in the 2 major drainages of that study area, suggesting a density of about 0.5/km². Also based on anecdotal observations during helicopter capture operations, elk were more abundant at Willapa Hills than Nooksack and Springfield, but local elk density was unknown.

METHODS

Our sampling reflected 2 main themes. First, we identified aspects of plant communities that directly influenced foraging behavior (e.g., forage selection patterns, time spent foraging each day, bite rates), nutritional responses (e.g., dietary DE and DP and intake rates of these nutrients), and, to a lesser degree, performance responses (e.g., body fat dynamics of adults and growth of calves). Second, we evaluated how relations between elk responses and vegetation varied among forest vegetation

zones and forest succession to understand the extent to which nutritional responses could be predicted.

We collected data in 349 macroplots at the 3 study areas that ranged in size from 0.4–5 ha, depending on data collection objectives (Table 2). In each macroplot, which was the sampling unit for all analyses of vegetation and elk foraging and nutritional responses, we measured overstory and understory vegetation and topography. We used captive elk in 89 macroplots to quantify relations among habitat conditions, foraging behavior, and nutritional responses. The macroplots were allocated among early, mid, and late seral forests and across a range of ecological conditions described in a potential natural vegetation (PNV) classification system for the region (Franklin and Dyrness 1988, Henderson et al. 1992). Such classification systems integrate effects of climate, topography, and soils on vegetation composition, abundance, and phenology (Franklin and Dyrness 1988, Henderson et al. 1992). Our approach emphasized successional and silvicultural influences on overstory and understory vegetation, foraging behavior, and nutritional regimes of elk within each of the major PNV types, and among the 3 physiographic provinces represented by our study areas. The final step was to develop equations to predict nutritional responses that reflected variation among PNV types, across successional sequences, and among study areas.

Using electric fences, we held 4 mother–calf pairs in 89 macroplots for either 7 days or 2–3 weeks. For the 7-day trials, we monitored foraging behavior, dietary quality, and nutrient intake rates across the duration of pen occupancy. However, we report data of foraging behavior and nutritional responses only for the first day of pen occupancy, assuming that data collected this first day would best represent wild elk behavior and nutrition (before

our elk altered plant communities appreciably). For the 2–3-week trials, we evaluated body fat changes and calf growth rate in each trial in relation to foraging and nutrition data collected during the trial.

We used captive elk ($n=25$) that were trained to be highly tolerant of close observation by field personnel (Cook et al. 1996) because much of the data we collected cannot be measured accurately with wild elk in forests. Captive elk and deer have long been used in foraging studies as proxies for their wild counterparts in native vegetation communities (Collins and Urness 1983, Wickstrom et al. 1984, Canon et al. 1987, Riggs et al. 1990, Parker et al. 1999). Diet selection does not differ significantly between captive and wild existence (Yarrow 1979, Austin et al. 1983, Olsen-Rutz and Urness 1987, Spalinger et al. 1997), nor do search times, bite rates, encounter rates, and other aspects of foraging (Olsen-Rutz and Urness 1987). Olsen-Rutz and Urness (1987) noted, however, that how supplemental feeding was integrated into experimental protocol may affect foraging behavior. Our elk subsisted almost entirely on native vegetation during the summer–early autumn sampling period, as they did late spring through early autumn in forests and rangeland communities in northeast Oregon the year before the study began. By using lactating cows with calves at heel, our animals were under high nutritional demands (Cook et al. 2004) that translated to greater foraging effort (Illius 1997) typical for summer and early autumn. We used a dependable bite-count technique to estimate intake rate (Renecker and Hudson 1985, Wairimu and Hudson 1993), and we minimized observer bias by limiting collection of diet data to 2 personnel (RC and JC) throughout the project. We conducted this research in accordance with an approved animal welfare protocol (Starkey

Table 2. Allocation of macroplot samples by potential natural vegetation (PNV) zone and seral stage at 3 study area in western Oregon and Washington, 2000–2002. All plots refer to total number of macroplots sampled with and without elk; plots with elk refer to macroplots where elk foraging was sampled. Early successional refers to stands ≤ 20 years in the western hemlock and Pacific silver fir habitat types, and, in the mountain hemlock series, stands dominated by seedlings or saplings and with low overstory canopy cover; closed canopy forests include all other stands and typically had high canopy cover ($>70\%$).

PNV/seral stage	Nooksack		Willapa Hills		Springfield		Total	
	All Plots	Plots with elk	All Plots	Plots with elk	All Plots	Plots with elk	All Plots	Plots with elk
Western hemlock-salal	7	3	5	1	61	20	73	24
Early successional	4	3	3	1	33	12	40	16
Closed-canopy forest	2	0	1	0	23	8	33	8
Thinned	1	0	1	0	5	0	7	0
Mean elevation (range)	189 (87–328)		452 (400–540)		627 (230–1,082)			
Western hemlock-swordfern	71	17	85	25	40	8	196	50
Early successional	30	10	35	15	12	3	77	28
Closed-canopy forest	25	0	40	6	25	4	90	10
Thinned	16	7	10	4	3	1	29	12
Mean elevation (range)	342 (96–697)		385 (114–680)		759 (295–1,213)			
Hardwood ^a	9	3	0	0	0	0	9	3
Mean elevation (range)	345 (141–780)							
Pacific Silver Fir	33	3	8	1	7	1	48	5
Early successional	14	2	3	1	2	1	19	4
Closed-canopy forest	14	1	5	0	4	0	23	1
Thinned	5	0	0	0	1	0	6	0
Mean elevation (range)	838 (530–1,156)		751 (487–976)		1,011 (650–1,403)			
Mountain hemlock	23	10	0	0	0	0	23	10
Early successional	14	7	0	0	0	0	14	7
Closed-canopy forest	7	2	0	0	0	0	7	2
Thinned	2	1	0	0	0	0	2	1
Mean elevation (range)	982 (720–1,217)							

^a Macroplots in which $>60\%$ of stems in the overstory were hardwood species, mainly red alder and, occasionally, big leaf maple (*Acer macrophyllum*). All hardwood stands were located in the western hemlock-swordfern type.

Vegetation Sampling

Classification of PNV types for the region occurred at multiple levels of detail including a series level reflecting dominant and regenerating tree species and, within each series, plant association groups reflecting dominant understory species (Franklin and Dyrness 1988, Henderson et al. 1992). We restricted our analysis to the series level (WHS, PSS, and MHS) because we had too few samples for meaningful replication within plant association groups. However, we divided the WHS into 2 subcategories, WHS-salal for the drier portions, and WHS-swordfern for the wetter portions of the WHS (Franklin and Dyrness 1988).

We classified stands into the PNV series by applying several criteria to our vegetation data sets. In older communities, we classified stands with >10% of stems in the live canopy consisting of mountain hemlock as MHS, with >10% of stems of Pacific silver fir as PSS, and with neither mountain hemlock nor Pacific silver fir as WHS at low to moderate elevations (Henderson et al. 1992). For highly disturbed early seral and young mid seral stands, we classified to series based on tree species naturally regenerating in the stand (Henderson et al. 1992), PNV type of adjacent older stands, and presence-absence of several understory indicator species that we derived from Henderson et al. (1992). We classified stands as WHS-salal if salal was more abundant than swordfern and WHS-swordfern if swordfern was more abundant.

We also identified stands that were dominated by hardwood trees, mostly red alder, as a separate type. These stands technically were not a PNV type because they occur as an intermediate stage in mid-succession (Franklin and Dyrness 1988). We included hardwood stands as an extra type because understory vegetation often differed from that of mid seral conifer stands. Hereafter, we generally refer to our vegetation categories—WHS-salal, WHS-swordfern, PSS, MHS, and hardwood stands—as habitat types.

We located macroplots for sampling vegetation across our study areas using random sampling within a geographic information system stratified among the 3 PNV types and 3 successional-structural stages (stand initiation that developed immediately after clearcut logging, mid seral stages including stem exclusion and maturing forests in the understory-reinitiation stage, and late seral stages; Oliver and Larson 1996). Because late seral stages were rare on our 3 study areas, we sampled an additional ~20 macroplots in late successional stands at the H. J. Andrews Experimental Forest near our Springfield study area. We placed macroplots within stands using a random starting point located ≥ 50 m from stand edges to reduce potential road and edge effects.

Macroplots used solely for vegetation sampling were 90 m by 50 m (0.45 ha). We measured vegetation and site characteristics along 5 parallel transects spanning the width of the macroplot and spaced 15 m apart from the ends of the macroplot. Along each transect, we placed 2 2-m² circular plots for sampling abundance of understory vegetation, 2 467.2-m² circular plots in sparse forests or 2 116.8-m² circular plots in dense forests for sampling density of tree stems, and 10 points located equidistant along each transect for measuring forest overstory with an ocular

sighting tube (moosehorn; Bunnell and Vales 1990, Cook et al. 1995). From the center of each large circular plot, we selected the 3 trees nearest the plot center, measured tree height with a laser hypsometer or clinometer and diameter at breast height, and recorded species for these trees plus the next closest 3 trees. At the center of each transect, we measured aspect, slope, stand dominant height (West 2004), and height to the bottom of the live canopy. Our suite of variables representing overstory conditions included canopy cover ($n=50$); stand dominant height ($n=5$); height to live canopy ($n=5$); diameter at breast height, basal area, and individual tree height ($n=30$ trees in 10 plots); tree density ($n=10$ plots), and tree composition ($n=60$ trees in 10 plots).

We estimated understory biomass for each plant species on each transect by clipping plants 1 cm to 2 m above ground to represent the foraging height of elk. We clipped current-year's growth of deciduous vascular plants and current year's growth plus all green foliage from conifers and evergreen shrubs from previous years (because elk occasionally consumed previous-year's green foliage). We sorted and bagged vegetation samples by individual species, oven-dried these at 75°C to a constant mass, and weighed dried samples.

To estimate forage quality, we collected plant material from the center of the first, third, and fifth transects. We separated the samples into 6 life-form groups (graminoids, forbs, deciduous shrubs, evergreen shrubs, shade-tolerant ferns [referred to as forest ferns], and bracken fern [a weedy fern that sometimes dominated early-successional stages]). We clipped plants nearest to the center of each transect in the same manner that we clipped biomass samples. However, we excluded conifers and previous-year's growth of evergreen shrubs, assuming that neither would compose more than minor levels in elk diets. This procedure overestimated DE in evergreen shrubs because it excluded tissue of the least palatable and coarsest plant material that was well represented in the abundance samples.

We placed plant material in 4-L sealable plastic bags, buried these under ice immediately after collection to stabilize cell solubles and aromatic compounds (Robbins 1983: 244, Minson 1990: 35), and transferred them to a freezer in ≤ 48 hours. The Wildlife Habitat Analysis laboratory at Washington State University processed the samples, including freeze-drying and detergent fiber assays (Goering and Van Soest 1970; Ankom Fiber Analyzer ^{200/220}, Ankom Technology, Fairport, NY, USA), to estimate percent dry matter digestibility (DMD as described by Robbins et al. (1987a, b):

$$\text{DMD} = \left(\left(0.9231e^{(-0.0451((\text{ADL}/\text{NDF}) \times 100))} - 0.030\text{AIA} \right) \times \text{NDF} \right) + ((-16.03 + 1.020(100 - \text{NDF})) - 2.8(11.82\text{BSA})),$$

where ADL is acid detergent lignin, NDF is neutral detergent fiber, AIA is acid insoluble ash, and BSA is precipitation of bovine serum albumin by tannins (mg of precipitate/mg of forage dry matter; Martin and Martin 1982). We calculated DE as $\text{DE} = \text{GE} \times \text{DMD}$, where GE is gross energy in kcal/g of forage determined by bomb calorimetry (C5000, IKA Works, Inc., Wilmington, NC, USA; Hobbs et al. 1982). We did not run BSA or GE assays on these forage quality samples to reduce costs.

Without these, our assays would provide an estimate of forage DMD without tannin astringency and could not be converted to estimates of DE. Therefore, we derived estimates of tannin astringency and GE for each plant life-form group and study area from elk diet samples (Appendix A). We used these estimates as constants reflecting tannin effects and GE in the above equations (Robbins et al. 1987a, b).

Forest Succession Patterns

Overstory and understory development.—We modeled forest development trajectories for canopy cover, stand dominant height (West 2004), basal area, tree density, diameter at breast height, and basal area using linear and nonlinear regression across 3 age categories: early through mid seral (1–75 years), mid through late succession (50–642 years—the latter our oldest stand), and overall models that depicted the entire successional sequence. We present detailed results only for canopy cover. We first used CurveExpert (CurveExpert 1.37, D. G. Hyams, Madison, AL, USA) to select appropriate regression types and initial parameter values and reran the best model (i.e., lowest standard error of the estimate [$S_{y,x}$] and least number of estimated coefficients) using nonlinear procedures (Gauss–Newton estimation method with PROC NLIN; SAS Institute 1988), least squares nonlinear methods, and least squares linear regression (PROC GLM; SAS Institute 1988). We plotted results with 95% confidence intervals by habitat type and study area to provide a qualitative perspective of differences in overstory development among them. We also modeled changes in percent composition in the overstory of western hemlock, Pacific silver fir, mountain hemlock, Douglas fir, and western red cedar, all other conifers combined, and all hardwood species combined over the entire data stream.

Data from our thinned macroplots ranged from 20–60 years, so we used all macroplots within this range to evaluate effects of thinning. For samples collected in the WHS, we initially used analysis of covariance (ANCOVA) to identify effects of thinning on our overstory variables, with stand age, thinning, study area, age \times thinning, and age \times thinning \times study area as covariates. If covariates reflecting age were insignificant, we used analysis of variance (ANOVA) to identify the main effect of thinning and the thinning \times study area interaction.

We illustrated successional trends in total understory abundance (kg/ha), composition changes in plant species, and forage quality. To identify similarities between the initial composition and changes in community composition over time, we calculated the mean composition of plant species during the first 4 years after clearcutting and used Kulczynski's similarity index (Oosting 1956, MacCracken and Hansen 1984) to track subsequent, community-wide compositional changes by habitat type and study area with the nonlinear modeling approach described above (i.e., CurveExpert and PROC NLIN). We then graphed composition by plant life-form groups to illustrate which plant groups most accounted for changes in community composition over time. As we did for evaluating effects of thinning on overstory, we initially used ANCOVA to identify thinning effects on abundance of total understory and each life-form group, with study area, age, thinning, stand age \times thinning, and study area \times thinning as covariates. If main and interaction effects of age were insignificant, we reran the analysis as a 2-factor

ANOVA, with only study area, thinning, and their interaction, and used least-square means to identify significant differences within study areas.

Forage quality development.—We conducted analyses in 4 steps to identify differences in DE among plant groups, study areas, and habitat types while controlling for influences of season (i.e., sampling date) and overstory canopy cover. First, we pooled data across study areas, because several of the habitat types were either not present or rarely encountered at several study areas (Table 2). We conducted an ANCOVA with the covariates habitat type, plant life-form group, and their interaction to identify their influences on DE, with date and overstory canopy cover included as covariates, and used least-square means to identify significant differences among plant life-form groups by habitat type. We conducted a second ANCOVA using only data from the WHS to evaluate effects of study area on forage DE, with plant life-form group, study area, their interaction, season, and canopy cover as covariates. We identified differences among study areas within plant groups using least-square means.

Second, we evaluated influences of season and forest overstory canopy cover on forage DE. We conducted 5 ANCOVAs, 1 each for graminoids, forbs, forest ferns, deciduous shrubs, and evergreen shrubs, with study area, habitat type, season, season \times habitat type, canopy cover, and canopy cover \times habitat type as covariates. We regressed DE of each plant life-form group with canopy cover by habitat type for those plant groups where effects of canopy cover or the canopy cover \times habitat type interaction were significant.

Third, we calculated community-wide DE for each macroplot as the average DE across plant groups weighted by the abundance of the plant groups, and developed forage DE successional profiles (i.e., an estimate of community-wide average DE for each habitat type across time) for study areas and habitat types. Because we collected forage-quality samples in 232 of 349 macroplots ($n=58$ at Springfield and 63 at Willapa Hills in 2001, and 111 at Nooksack in 2002), we estimated DE for macroplots not sampled for DE from estimates obtained from macroplots with DE sampling in several steps: 1) we calculated mean DE for each plant group by habitat type (separately by study area for the WHS-swordfern type and pooled among study areas for the other habitats), 2) overstory canopy cover classes ($<70\%$ and $\geq 70\%$), and 2 seasons (summer = late Jun–Aug; autumn = >15 Sep–31 Oct); and 2) we used the appropriate DE mean of each plant group based on canopy cover class, season, habitat type, and study area, and weighted it by relative abundance of each plant life-form group in the unsampled macroplot to estimate DE. We executed these steps separately for summer and autumn.

Finally, we presented estimates of community-wide forage DE levels across succession in terms of abundance of understory vegetation partitioned into 1 of 4 nutritional value classes presented for lactating female elk in summer and early autumn by Cook et al. (2004): 1) excellent = vegetation with DE levels ≥ 2.90 kcal/g that present virtually no nutritional limits to elk in summer and early autumn; 2) good = DE levels ≥ 2.75 – 2.90 kcal/g that impose only minor nutritional limitations on reproductive and survival performance; 3) marginal = DE levels ≥ 2.40 – 2.75 kcal/g that may significantly reduce reproduc-

tive performance; and 4) poor = DE levels <2.40 kcal/g that may greatly reduce probability of reproduction and survival. We present the data graphically for the 2 WHS types combined and PSS and MHS combined for summer and autumn.

We determined effects of thinning on DE of each plant group and the average of the plant community generally as we did for thinning effects on overstory and understory described above. We used either ANCOVA or ANOVA, depending on age influences in an initial ANCOVA, to identify thinning effects on forage DE levels. We used only those macroplots for which we sampled DE levels.

Foraging Experiments

General field procedures.—We selected pen locations (i.e., pen = macroplot with elk) to be well-interspersed (Hurlbert 1984) across study areas and to provide a diverse cross-section of plant communities for evaluating relationships between plant community characteristics and foraging-nutritional responses of elk. We selected random coordinates across our study areas and evaluated these for logistical suitability (e.g., accessible by roads adequate for large trailers in areas rarely used by the public). For those found to be suitable, we constructed a cluster of 2–3 pens, with each pen usually in a different seral stage in relatively homogenous habitat as near as possible to the suitable random point (grouping the pens facilitated protection from predators and the public). We stratified the study areas into high- and low-elevation categories, and normally operated 1 cluster in each elevation stratum simultaneously. In some instances, we rejected potential pen sites with very dense overstories for sampling with elk, because virtually no suitable forage was present. We found early in the study that avoiding placing pens in stands with virtually no suitable forage was inhumane and thus violated our animal welfare protocol.

Pen sizes varied inversely with forage density to provide roughly equal amounts of total forage in each so that foraging dynamics would be a function of forage characteristics (i.e., forage density [kg/ha], quality, composition). We used 3 main criteria to determine pen size, with the first being the most crucial: 1) provide sufficient forage such that abundance, particularly of preferred species, would largely be unaffected by forage offtake the first 12–18 hours of pen occupancy; 2) hold reasonably constant the total amount of forage across all pens; and 3) sized to document changes in foraging dynamics as a function of forage removal over the time that the elk were in the pen (the latter to be reported elsewhere). The 7-day pens normally ranged in size from 0.4–1.7 ha, although several sampled in the first few months of the study were ~ 0.2 ha (before we realized that elk strongly avoided large proportions of available forage). Our objective for pens in which we measured changes in body fat and calf growth was to have pens large enough that suitable forage species remained available over the 2–3 weeks that elk were in the pen. These also varied inversely in size with vegetation abundance and ranged from 1.7–5 ha.

We released 4 female elk and their calves into pens late in the day and allowed animals to adjust to each new location before data collection began at first light the next morning. One observer recorded activity data and another recorded number of bites by plant species and measured distance traveled while feeding, using

techniques developed during pilot trials with the elk during summer 1998 (J. G. Cook and R. C. Cook, National Council for Air and Stream Improvement, unpublished data). Among these developments was a clear need to restrict sampling of foraging to 2 experienced investigators. In addition, we also found that foraging behavior (mainly bite and travel rates, forage selection patterns) were similar among morning, mid-day, and evening foraging bouts. Hence, we could sample foraging behavior during subportions of the day and apply these data for other portions of the day. We confirmed the latter by sampling foraging all day at Willapa Hills and Nooksack and testing for time-of-day and study area effects using 2-factor, repeated-measures ANOVA (PROC MIXED; SAS 1993).

Observers monitored elk activity continuously from first light until dark. We used automated, motion-sensitive accelerometers (actiwatches; Mini-mitter Corporation, Sunriver, OR, USA; Naylor and Kie 2004) at Willapa Hills ($n=6$ units) and Nooksack ($n=2$ units) attached to elk radio-collars to account for activity at night.

We collected bite data using standard bite-count methods (Collins and Urness 1983, Wickstrom et al. 1984, Canon et al. 1987, Riggs et al. 1990, Gillingham et al. 1997, Parker et al. 1999) during 2, 20-minute trials per elk in the early morning. The observer selected an initial elk at random and recorded plant species of each bite during the 20 minutes with a tape recorder, and selected subsequent elk in sequence of their ear tag numbers. We measured distances traveled while foraging using a rolatape (Rolatape[®], Watseka, IL, USA). We also sampled bite mass, bite rate, and intake rate during 60 additional trials at Willapa Hills and Nooksack during mid-day and early evening to confirm that foraging intensity during feeding bouts was similar across the day, as we found in our 1998 pilot trials.

We selected the 20-minute trial duration based on observations during the pilot study. Relatively long trials better averaged across bursts and lulls in foraging rate (Gillingham et al. 1997) but were more likely to be interrupted by changes in activity—the 20-minute trials provided a good compromise. If elk terminated foraging during the 20 minutes, we used a 3-minute rule: 1) if the elk ceased to forage for >3 minutes, the grazing bout was stopped and the observer moved to the next elk, returning to finish the trial once the elk resumed foraging (without prematurely ending a subsequent trial); 2) if the elk paused in foraging but resumed in <3 minutes, the trial continued without interruption; and 3) if, because of interruptions in foraging, the 20-minute trials were divided among 2 or more feeding bouts, data were used only if the feeding bout was >3 minutes.

We downloaded the recorded data immediately upon completion of the 8 trials (i.e., 4 adult females \times 2/day) and calculated overall dietary composition by plant species (bites recorded on each species/number of bites recorded). We clipped and bagged 10 simulated bites of each consumed species to represent specific plants part consumed (e.g., flowers, berries, leaves, stems, current year's and previous year's growth). We oven-dried the simulated bites at 75°C and weighed them to estimate bite mass. We assumed equal, within-species bite mass among elk within pens.

We collected simulated diet samples for nutritional assays separately for each elk (i.e., $n=4$ samples/pen/day). For those species representing in aggregate at least 90% of elk diets, we

collected ≥ 20 simulated bites of plant species in the diet in the same proportions selected by each elk. We sealed the composited samples in 4-L plastic bags, immediately buried them in ice, and transferred them to a freezer within 2 days. The Habitat Analysis Laboratory at Washington State University estimated DE (see above), where DMD, GE, and BSA precipitation were estimated as described by Robbins et al. (1987a, b). Nitrogen content (%) of diets was estimated using a Carbon-Nitrogen TruSpec analyzer (LECO; St. Joseph, MI, USA) and converted to DP as per Robbins et al. (1987a, b).

Dietary composition and selection.—We calculated the amount consumed (g/trial) of each species in the diet as the product of the number of bites taken and average bite mass of that species for each elk, calculated composition for each elk, and averaged consumption and composition data across the 4 elk in the pens for subsequent analyses. We estimated selection by elk for each vascular plant species from macroplots in which the species was present, whether the elk ate it or not, using Ivlev's electivity index and Chesson's selective indices (Manly et al. 1993):

$$\text{Ivlev} = (\% \text{ of diet} - \% \text{ available}) / (\% \text{ of diet} + \% \text{ available});$$

$$\text{Chesson} = (\text{diet composition} / \text{available composition}) /$$

$$(\Sigma(\text{diet composition} / \text{available composition of all taxa})).$$

Ivlev's index ranges between -1 and $+1$, with $+1$ indicating strong selection, -1 indicating strong avoidance, and 0 indicating neither avoidance or selection (i.e., neutral), and thus provides a simple and practical depiction of selection particularly for management purposes. Chesson's index ranges between 0 and 1 and provides an estimate of the probability that the next bite will be of the i^{th} species, and thus may have greater value for modeling than Ivlev's. We evaluated significance of selection of individual plant species across all macroplots with 2 methods. First, we used Student's t value to identify which plant taxa had an Ivlev's value that differed from 0 (PROC MEANS; SAS Institute 1988). We considered plant species avoided if they had a negative Ivlev index that differed from 0 ($P \leq 0.10$), selected if they had a positive Ivlev's index at $P \leq 0.10$, and neutral (i.e., use = availability) if they failed to differ significantly from 0 . Second, we used the non-parametric sign rank test to test which plant taxa had an Ivlev's value that differed from 0 (PROC UNIVARIATE; SAS Institute 1988). For each, the number of pens where the species was present served as the sample size ($n = 1$ to 89 , depending on species). We ran both analyses to compensate for shortcomings of each, that is, lower power of the non-parametric test and strong non-normality of some plant species for the parametric test. When results using both tests differed, we relied on our anecdotal observations of elk responses in the field to make a final decision.

We used plant life-form groups rather than individual species to evaluate potential differences in selection patterns among seasons and study areas because the groups were present in all pens. We calculated Ivlev's index (dependent variable) for each plant life-form group and conducted a fixed-effects, repeated measures 3-way ANOVA with plant life-form group, season (summer vs. autumn), study area, and all 2- and 3-way interactions of these covariates. We used PROC MIXED with plant group as the repeated variable of the analysis (i.e., multiple measures from the

same pen), and we used Akaike's Information Criterion, corrected for small sample size (AIC_c), to select the best-fitting error structure from those deemed biologically appropriate (see Verbeke and Molenberghs 2000); error structures considered were simple or variance component, compound symmetry, spatial power, spatial Gaussian, and spatial exponential. Of primary interest in this analysis was the season \times plant group and study area \times plant group interactions. We used least-square means to identify significant differences among components of the interaction terms.

We evaluated the extent to which diet composition, abundance in the plant community, and bite mass (dependent variables in 3, 1-way ANOVAs) differed among the 3 forage selection groups (i.e., avoided, selected, neutral). Individual plant species served as replicates for this analysis, where for each species we included its percentage of diet, abundance (kg/ha), and bite mass averaged over all pens where they occurred. We limited this analysis to those plant species that composed either $\geq 1\%$ of diet composition or $\geq 1\%$ of community composition across the entire data set. For significant ANOVAs, we used the Student Newman-Keuls range test (SNK) to identify differences in the 3 dependent variables among the 3 selection categories. We then reformulated this analysis to compare differences in the 3 dependent variables among plant life-form groups. Finally, we present abundance of selected, neutral, and avoided plants by forest stand age to illustrate changes in abundance of these 3 plant categories across succession.

Foraging dynamics.—We partitioned our measures of foraging dynamics into 4 general classes—activity, foraging behavior, dietary quality, and nutrient intake rates—and evaluated each as functions of habitat conditions available to the elk. Activity categories included feeding, ruminating, and feeding + ruminating. Because we were unable to detect rumination accurately with the actiwatchers, we analyzed observer-collected data on feeding and ruminating times for daylight hours; we also evaluated feeding time for 24-hour periods.

We converted actiwatch values to activity categories by coupling direct observations during the day by field personnel with actiwatch values recorded concurrently (Naylor and Kie 2004) for each pen. We manually selected relatively long periods of uninterrupted activity within our activity categories from our direct observation data and paired these with actiwatch activity values for the same blocks of time. These calibration data sets typically contained 1,200–1,800 1-minute samples of elk activity collected over the week of pen occupancy.

Inactive actiwatch values were the lowest, foraging values usually fell into a middle range, and non-foraging active usually were the highest values. Thus, we calculated bounds (i.e., breakpoints) around mean actiwatch values for feeding using an iterative process to separate foraging from inactive and non-foraging active. We calculated 7 sets of upper and lower bounds around the mean as multiples of the standard deviation (i.e., ± 0.8 SD, ± 1.0 SD, ... ± 2.0 SD). These bounds sometimes varied substantially among pens, so we calculated separate breakpoints for each pen. We then calculated the correct classification rate of observed activity for each set of bounds. We selected the upper and lower bounds (i.e., the multiple of SD) that provided the highest correct classification rate for the 3 activities using the

training data set for final prediction of elk activity for each pen. Finally, using the entire set of observed activity data, we compared predicted percent time in each activity category with observed percent time each day in each pen to estimate correct classification rate.

Dependent variables of foraging behavior included speed of travel while feeding, bite mass, bites/meter of travel, bites/minute, and intake of forage dry matter/meter of travel. We calculated travel rate as meters traveled during the foraging trial divided by time of the trial, bite mass as the overall average bite mass in the pen (a weighted average of number of bites by plant species and bite mass of each species), bite rate as the number of bites taken per trial divided by time of the trial, and bites/meter as the number of bites taken per meter traveled during the trials. We calculated dry matter intake per meter as the number of bites \times mean bite mass divided by distance traveled during the trials. Dependent variables of dietary quality included tannin astringency (mg of BSA precipitated/mg of dry matter), DMD (%), DE (kcal/g of forage consumed), and DP (%). We calculated dependent variables of intake rates on a per-minute and 24-hour basis for forage dry matter (DM), DE (kcal), and DP (g).

We conducted a series of ANCOVAs to clarify how various habitat attributes affected each of our foraging response variables. We evaluated 8 covariates for each foraging variable: study area, habitat type, thinning, successional stage, date, canopy cover, stand age, and forage groups including abundance of avoided (AvdSpp), neutral (NeuSpp), and selected (SelSpp) species, and all species combined (AllSpp). Including all 8 covariates, plus interaction terms, into a single ANCOVA for each foraging response variable would have been untenable because of insufficient sample size ($n = 89$). Also, different subsets of the data were required to evaluate several of the covariates of interest, thus requiring separate ANCOVAs. Therefore, each ANCOVA included the covariate of interest plus 3 or 4 additional covariates with the intent to control for the effects of these additional covariates as follows: 1) study area (the covariate of interest) plus habitat type, thinning, date (month number + [day/31.1]), and canopy cover (%); 2) thinning plus study area, habitat type, and date; 3) habitat type plus study area, thinning, date, and canopy cover; 4) seral stage plus study area, habitat type, and date; 5) date plus study area, habitat type, thinning, and canopy cover; 6) canopy cover plus study area, habitat type, thinning, and date (with 5 and 6 in the same regression run); 7) stand age (years) plus study area, habitat type, thinning, and date; and 8) AvdSpp, NeuSpp, and SelSpp plus study area, and date and an alternative ANCOVA with AllSpp plus study area and date. With a total of 18 foraging response variables, this analysis step consisted of 144 ANCOVAs. We used least-square means to identify which means differed for each significant categorical variable of interest.

We included several variations on this baseline strategy. For each of the 144 ANCOVAs, we first ran 2 ANCOVAs, 1 with all possible 3-way and 1 with all possible 2-way interactions of the covariates, with main effects of each covariate excluded. This screening exercise to identify important interactions was necessary because of low sample size, and because stepwise statistical procedures exclude categorical and continuous variables together. We included only the significant interaction terms in the subsequent ANCOVAs with main effects of the covariates,

and excluded these interactions if they no longer remained significant with main effects included.

Additionally, we evaluated the effect of study area on each dependent foraging variable using only those macroplots sampled in the WHS, because only this series was well represented across all 3 study areas (Table 2). We evaluated the main effect of thinning with ANCOVAs using those macroplots ranging in age from 20–60 years (the age range corresponding to that of thinned stands in our sample), and again included only those samples in the WHS. We evaluated influences of our 4 habitat types on foraging responses, and ran the ANCOVAs with the full data set excluding hardwood stands. We included 3 seral stages in our analysis of the successional stage covariate: early seral stands (regeneration and sapling stages generally with $<70\%$ canopy cover), closed-canopy forests (mid and late seral stages with $\geq 70\%$ canopy cover), and thinned stands regardless of canopy cover. We excluded the hardwood stands in our sample from the successional stage analyses because of low sample size ($n = 3$).

For our continuous covariates (date, canopy cover, and stand age), we anticipated nonlinear relations with many of the foraging response variables, and we used a residuals analysis to evaluate this potential. Once we completed the final ANCOVA, we then removed the continuous covariate of interest, reran the ANCOVA, and generated residuals. We added the residuals to the overall mean of the dependent variable, such that the scale of the residuals would match that of the original data to better illustrate the relationship. We used CurveExpert with the residuals to identify nonlinear relationships and appropriate model types between the continuous covariates and foraging response variables and reran the analysis in PROC NLIN to provide a P value for the relationship. This strategy produced 2 P values for each of the 3 continuous covariates, 1 from the initial ANCOVA and 1 from the regression analyses on the residuals. We considered the relationship to be nonlinear if the P value from the residuals analysis was lower than that from the ANOVA. If the regression relation was linear, the P value from the original ANCOVA was appropriate; if the relation was nonlinear, the P value from the regression was of interest. In cases of significant interactions among covariates, we removed both components of the interaction term from the ANCOVA to conduct the residuals analysis. For the analysis where stand age was the covariate of interest, we omitted 1 very old stand from the analysis, because it was markedly older (200 years) than any of the other samples, and thus it had an overbearing effect on results.

Using the final ANCOVA for each forage response variable and the various covariates, we added the mean community-wide forage DE in the pen and the interaction of abundance of NeuSpp plus SelSpp (i.e., AccSpp) and mean DE of these species (presumed equal to the DE of grasses, forbs, and deciduous shrubs [DE-GFS]). We emphasized this interaction because even very high DE of these species may have little bearing on elk foraging if the abundance of these species was very low. We added this analysis as a supplemental step because we collected forage quality data only for a subset of pens ($n = 60$ of the 89, all from Nooksack and Willapa Hills). Finally, because rumination and feeding times may be affected by dietary quality and dietary fiber levels (Illius 1997), we added the covariates NDF, acid detergent fiber (ADF), dietary DE, and dietary DP into the final

ANCOVAs for feeding and rumination time, 1 covariate at a time, to evaluate the influences of these forage quality covariates on feeding and rumination time.

We added another step in our analyses of dietary DP and intake rate of DP. Results for these 2 nutritional response variables from the analyses protocol described above were highly complicated and seemingly illogical. We evaluated the possibility that dietary DP levels were substantially influenced by soil moisture because the highest levels of DP in our data set, particularly after mid-summer, were in macroplots with unusually wet soils, and because protein levels in plants are known to reflect site factors (soil moisture and nitrogen; Van Soest 1994). We conducted stepwise regression with backward elimination (with significance level to remove at 0.025) to identify individual species of plants related to DP, which in turn might be indicators of soil moisture and nitrogen. Abundance of each plant taxa in our data set was included, along with date, overstory canopy cover, and abundance of selected (SelSpp), neutral (NeuSpp), avoided (AvdSpp), and accepted species (AccSpp = SelSpp + NeuSpp).

We designed an analysis to understand the relative contribution of the foundation variables (i.e., bite rate, bite mass, 24-hour feeding time, dietary DE, and dietary DP) to per-minute and 24-hour intake of DM, DE, and DP because variation in the derived variables depends on variation in each of the foundation variables (e.g., bite rate may affect estimates of forage intake rate, but if bite rate is constant among macroplots, then it accounts for no variance in intake rate). We added date and study area and first ran an ANCOVA to identify study-area effects, 1 ANCOVA for each intake variable. We expected that study area and date would be non-significant in these runs largely because neither was used to calculate the derived intake variables, unless we had discrepancies in our data sets among seasons or study areas (e.g., undercounted bites or overestimated bite mass at 1 study area). Hence, this step provided a check of methodological consistency among study areas. Then, dropping study area and date, we ran multiple regression and used standardized regression coefficients for each of the 5 independent variables (i.e., foundation variables plus date) as a measure of the relative contribution of each variable to intake rate of nutrients.

As a summary step, we presented our results for dietary DE and DP and intake dynamics of DE and DP by seral stage and habitat type along with estimates of nutritional requirements for lactating elk in summer. Additionally, we conducted an analysis of forage abundance in macroplots with elk versus those without elk in early seral and closed-canopy forests to evaluate the potential for biases in pen-site selection (i.e., to determine if our efforts to avoid placing elk in pens with unusually poor forage conditions resulted in a sampling bias in our data). We conducted a 3-factor ANOVA, with successional stage (early seral vs. closed-canopy forests), use of elk at the macroplot, and study area as factors. We used least-square means to identify differences between elk-sampled and elk-unsampled macroplots at each study area.

Foraging Experiments: Body Fat and Calf Growth

Fifteen of our 89 pens were designated for evaluating relationships of dynamics of body fat and calf growth with forage attributes and elk nutrition during summer through mid-

September, 6, 5, and 4 pens at Nooksack, Willapa Hills, and Springfield, respectively. We held elk for 2 weeks (3 weeks at Springfield). We measured adult body fat and calf mass when we released animals into the pens and again when we removed them from the pens 2 (3) weeks later. Pen sizes in the 2–3-week trials were larger than in the 7-day trials to avoid appreciable changes in foraging dynamics due to cumulative forage removal, and again varied in size inversely to total forage abundance (kg/ha) to hold a roughly constant total amount of forage available to the elk in each pen (pen size [ha] = $4.6 - 0.0036 \times \text{understory abundance [kg/ha]}$); $r^2 = 0.65$). In practice, it was logistically untenable to build pens large enough to hold constant total understory biomass in those pens with relatively little vegetation per unit area, and we expanded our analyses to include both total amount of vegetation (kg/pen) and forage density (kg/ha). Also, calves occasionally foraged outside the pens, particularly in late summer.

We weighed adult females and calves in a chute placed on portable electronic scales at the beginning and end of pen occupancy. At the same time, we estimated ingesta-free body fat (IFBF) in the adults via LIVINDEX, an arithmetic combination of maximum rump fat thickness (measured using a Sonovet ultrasound with a 5.0 MHz, 7.0-cm probe; Universal Medical Systems, Bedford Hills, NY, USA) and a body condition score (Cook et al. 2001). We expressed calf growth as change in kilograms per day of the trial, and change in IFBF as a percentage point change in IFBF per day of the trial. We collected elk foraging data 4 times spread equidistant from the first to the last day of pen occupancy.

We used forage abundance by forage selection categories, mean levels of dietary DE and DP, and mean per-minute intake rates of DE and DP over the time of pen occupancy to evaluate changes in nutritional condition and calf growth. Limited sample size restricted the scope of analyses. We first conducted a 2-factor ANOVA with study area and successional stage as factors, 1 for each animal performance variable (we present means but did not test effects of habitat type, primarily because we had only 3 pens in the PSS and MHS). We conducted stepwise regression with backward elimination (with P to remove at <0.15) to identify the best 2-variable multiple regressions using calf growth and IFBF change as dependent variables. Covariates included in the regressions included 1) dietary DE and DP and per-minute intake of DE and DP of the mothers averaged over the entire trials; 2) abundance (kg/ha) of AvdSpp, NeuSpp, SelSpp, AccSpp, and abundance of all species combined (AllSpp); and 3) abundance (kg) per elk-use day (number of days \times number of adult elk [$n=4$] in the pen) of AvdSpp, NeuSpp, SelSpp, AccSpp, and AllSpp. We ran 2 sets of these, the first using date and the nutrition variables (i.e., dietary DE, DP, and their per-minute intake levels) as independent variables and the second using date and the forage biomass variables (kg/ha and kg/pen of AvdSpp, NeuSpp, SelSpp, AccSpp, and AllSpp) as independent variables. We evaluated nonlinearity of the continuous covariates with CurveExpert.

Nutrition Models

We produced equations to predict 4 nutrition attributes (i.e., dietary DE and DP, and intake rates/min of DE and DP) of plant communities across the successional sequence in the WHS-salal,

WHS-swordfern, and the PSS and MHS combined. We used the equations to predict nutritional responses for macroplots without elk, ultimately to more fully illustrate nutritional value for elk across the successional sequence for our habitat types. Also, given the logistical constraints for using tame elk, we were unable to replicate sampling with elk sufficiently in many stand conditions (e.g., old-growth forests, stands with very dense overstories with little understory vegetation) but nevertheless acquired better replication in our vegetation-only macroplots. We reasoned that if we could adequately quantify relations between forage conditions and nutritional outcomes using elk, then we could use these relations to predict nutritional responses in stand types undersampled with elk but where we adequately sampled vegetation attributes.

We used stepwise regression with backward elimination to identify those predictor covariates that significantly contributed to prediction, and we used $S_{y \cdot x}$ to identify the best overall models. We used results from the above-described analyses to help identify important habitat variables for the prediction equations.

Covariates included abundance of plant groups based on plant life form and elk selection (AvdSpp, NeuSpp, SelSpp, AccSpp), date, dummy variables representing study area and high-elevation (PSS and MHS combined) versus low-elevation habitat types (WHS-salal and WHS-swordfern combined), and several additional variables reflecting site conditions that may affect nutrient levels in forage. We used plant indicators of wetter soil conditions based on the sum of abundances (kg/ha) of swordfern, red alder, lady-fern, and salmonberry (Franklin and Dyrness 1988, Pojar and MacKinnon 1994). We also used abundance of salal as a dry site indicator (Franklin and Dyrness 1988).

Once we selected the equations, we conducted a simple test as a check for errors that might lead to consistently biased predictions. We compared observed versus predicted values of nutrition for 1) early successional stages and closed-canopy forests within study areas in the WHS low-elevation habitats; 2) early successional and closed-canopy forests across study areas in the PSS and MHS habitats; and 3) thinned and unthinned forest in WHS habitats with stand age limited to 20 to 60 years. For each predicted-observed pair, we calculated a paired-difference t -test for significant differences from zero (i.e., if the predictions contained a bias). We conducted the t -tests for each combination of successional stage, study area, and habitat type.

As a final step, we used the final nutrition equations to graphically describe successional patterns of dietary DE and DP and intake per minute by study area and habitat type. For these equations, we used habitat data collected at all study plots ($n = 349$) to drive the nutrition prediction equations and plotted the predicted nutrition values against stand age. We separately predicted nutrition levels for our hardwood macroplots and for macroplots located in WHS habitats by study area in thinned and unthinned stands ranging from 20–60 years (the range in stand age for which we had data in thinned stands).

RESULTS

We sampled 349 macroplots across our 3 study areas: 143 at Nooksack, 98 at Willapa Hills, and 108 at Springfield (Table 2). The 3 forest series (WHS, PSS, and MHS) were common and frequently encountered in the Nooksack study area, whereas the

MHS was absent and the PSS was infrequent at our Springfield and Willapa Hills study areas. The WHS-salal type was most common in our Springfield sample, where warmer and drier climate prevailed. Frequency of WHS-salal, WHS-swordfern, PSS, and MHS were arrayed along an elevation gradient, a trend consistent with precipitation and temperature affinities for these types (Franklin and Dyrness 1988, Henderson et al. 1992).

We sampled hardwood stands only within WHS-swordfern stands at Nooksack (Table 2). Composition of hardwoods based on individual tree stems of the canopy layer was $\geq 65\%$ versus $\leq 35\%$ in coniferous stands, reflecting our criteria for designating hardwood stands. Red alder composed $>90\%$ of the hardwoods, and 5 of the 9 hardwood macroplots were located on wet sites from 100–200 m in elevation; the others were spread equally from 330–780 m.

Forest Successional Patterns

Overstory development.—After logging, site preparation, and planting to conifers, canopy cover developed in a sigmoid pattern over the first 75 years in all habitat types reflecting an initial delay, a rapid increase, and a plateau soon thereafter (Fig. 3; Appendix B). Canopy cover was 20–40% at 9–11 years in the WHS at each study area, and achieved a maximum of about 90% 18–20 years post logging at Nooksack and Springfield and 13–15 years at Willapa Hills. Only at Springfield did our sample size for both the swordfern and salal types in the WHS justify separate modeling for each type—results indicated similar canopy cover dynamics during early to mid-succession (Fig. 3, inset). Canopy was slower to develop in the PSS and MHS—the plateau of 90% required about 45 years in the PSS, whereas canopy cover reached only about 75% in stands of about 45 years old in the MHS (Fig. 3). Also evident in the full data set was a period of slow decline in canopy cover to approximately 80% in stands >100 years old (Fig. 4; Appendix B). Canopy cover in the MHS achieved 75–80% but may require at least several centuries to do so, if ever (Fig. 4, inset), likely depending on site conditions.

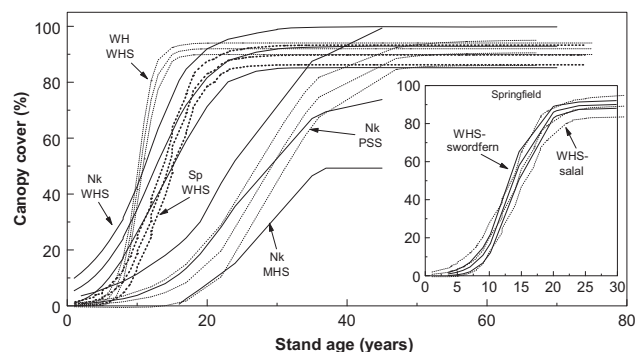


Figure 3. Development of overstory canopy cover in early stages of succession at Nooksack (Nk), Willapa Hills (WH), and Springfield (Sp) study areas in western Oregon and Washington, 2000–2002. Habitat type codes are WHS = western hemlock series; PSS = Pacific silver fir series; MHS = mountain hemlock series; WHS-salal = western hemlock-salal plant association; and WHS-swordfern = western hemlock-swordfern plant association. Canopy development is shown for the first 75 years of succession for the WHS, PSS, and MHS and, in the inset, for the first 30 years in the WHS-salal and WHS-swordfern habitat types. Regression lines and 95% confidence intervals are presented for each habitat type (see Appendix B for corresponding regression equations).

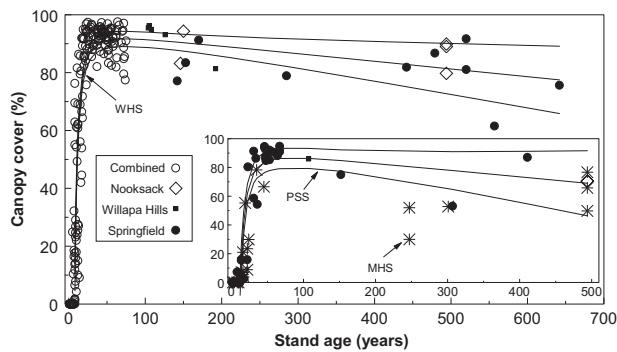


Figure 4. Development of overstory canopy cover across succession in the western hemlock (WHS), and in the inset, for the Pacific silver fir (PSS) and mountain hemlock (MHS; asterisks) habitat types at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Regression lines and 95% confidence intervals are presented for each habitat type (no significant relationship was found and no regression lines were presented for the MHS; see Appendix B for corresponding regression equations).

Development of other overstory variables across habitat types differed in several respects. For example, stand height developed linearly and achieved a maximum of 35–45 m at 70–80 years in the WHS, 100–120 years in the PSS, and up to 300 years in the MHS. Tree density generally doubled in the first 10–20 years, ranging from 1,500–4,000 trees/ha, declined over the next 70–80 years, and stabilized thereafter at 500–1,000 trees/ha. Basal area developed in a sigmoid pattern during the first 60–70 years in the WHS and PSS similar to that for canopy cover. Plateaus in the WHS were achieved at roughly 75 m²/ha in about 40 years at Willapa Hills and 50–75 years at Nooksack and Springfield and was thereafter markedly variable, ranging from 40–150 m²/ha. Development of basal area was slower in the PSS and MHS types, with 50–100 years in the PSS and longer in the MHS to achieve plateaus of about 80 m²/ha and 40–70 m²/ha, respectively. In general, relative abundance of Douglas fir and hardwoods declined and western hemlock and western red cedar increased over time in the WHS, with more rapid trends at Willapa Hills than Nooksack or Springfield (Appendix C).

Reductions in overstory due to thinning were modest in our 36 macroplots (Table 2) versus unthinned macroplots in the WHS. Canopy cover in thinned stands averaged 5–10% lower ($P < 0.001$) than in unthinned stands of the same age range; effects of stand age, study area, and their 2- and 3-way interactions with thinning were insignificant ($P > 0.30$; Fig. 5A). Diameter at breast height tended to be greater in thinned than in unthinned stands at Springfield and Willapa Hills ($P = 0.091$; Fig. 5B); no 2- or 3-way interactions with thinning were significant ($P > 0.28$). Basal area typically was higher in unthinned stands, but the effect increased with stand age ($P = 0.024$ for the age \times thinning interaction); no other main or interactive effects were significant ($P > 0.14$; Fig. 5C). We found little evidence of a thinning effect on stand height, tree composition, height to live crown, canopy volume, or tree density.

Understory development.—Understory characteristics were dynamic across succession and habitat types. In the WHS, understory vegetation averaged about 1,500 kg/ha in the first

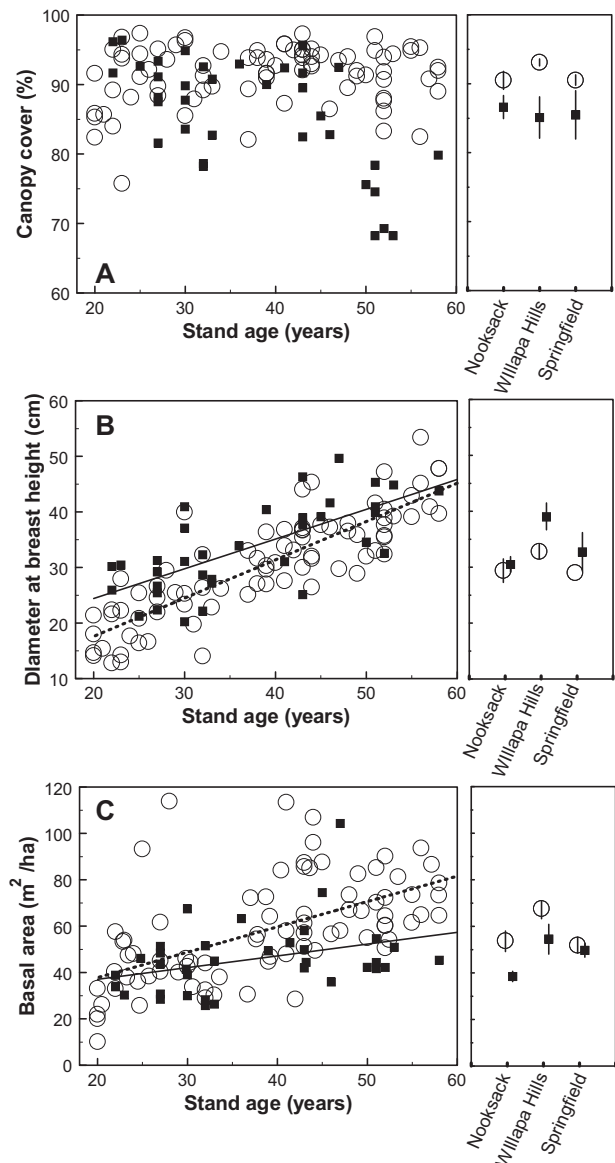


Figure 5. Overstory canopy cover (A), diameter at breast height (B), and basal area (C) in commercially thinned (solid squares, solid lines) and unthinned (open circles, dotted lines) stands in western hemlock forests (WHS) at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. The left panel shows overstory estimates plotted with stand age with data from the 3 study areas combined; regression lines indicate significant ($P \leq 0.05$) relations. The right panel presents the mean (± 1 SE) for each study area.

3–4 years after stand initiation, followed by 4 mostly distinct stages: 1) rapid increase to about 2,500 kg/ha during a period of peak production that lasted through 12–15 years after stand initiation; 2) rapid decline that ended at 25 years after stand initiation; 3) consistently low biomass of 100–500 kg/ha through age 45 that was among the lowest observed across the entire successional sequence; and 4) modest recovery of understory vegetation to 200–1,000 kg/ha in stands 45–90 years old. Thereafter (> 90 years old), total abundance ranged between 100–500 kg/ha (Fig. 6A). In the PSS and MHS, we observed a similar pattern through mid-succession, except that the amount of time required for transitioning among the stages was longer

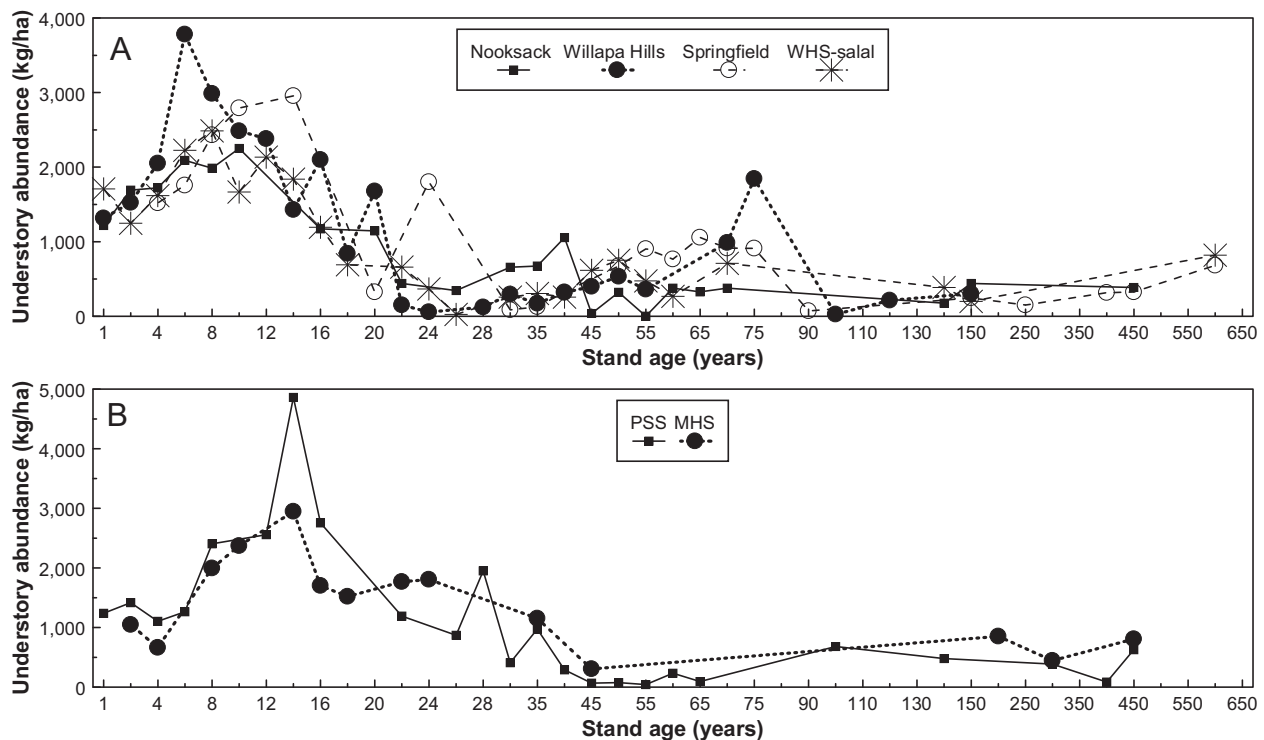


Figure 6. Understory vegetation abundance in the western hemlock-swordfern habitat type at Nooksack, Willapa Hills, and Springfield study areas and the western hemlock-salal (WHS-salal) habitat type combined across the 3 study areas (A); and the Pacific silver fir (PSS) and mountain hemlock series (MHS) across the 3 study areas (B).

(Fig. 6B). In the 9 hardwood stands at Nooksack, total understory abundance ranged from 525–900 kg/ha (Fig. 7A), moderately higher than in coniferous forests in the same age range.

In the combined WHS-salal and WHS-swordfern types, thinned stands contained more understory vegetation than did unthinned stands ($P=0.015$). Although the study area \times thinning interaction was not significant ($P=0.12$), the thinning effect was evident at Nooksack and Willapa Hills but not at Springfield (Fig. 7B; Table 3). In the PSS, understory abundance did not differ ($P=0.14$) in thinned and unthinned stands (Table 3).

Rapid changes in plant species composition occurred in the first 25 years after stand initiation, stabilized the next 25–50 years, and remained relatively constant thereafter based on Kulczynski's similarity index (Fig. 8). This pattern was consistent among all habitat types and study areas, although the greatest change in species overlap from early seral to older stands evidently occurred in the warmer and drier WHS-salal overall and the WHS-swordfern habitats at Springfield. We note, however, that our sample size of stands ≥ 100 years old was small, considerable variation existed in our overlap estimates in older stands, and the model of species overlap once stabilization had occurred was strongly influenced by the few samples we had in very old stands.

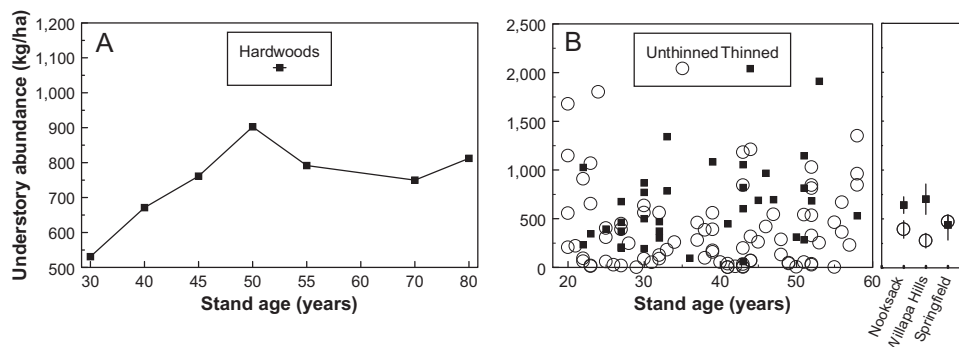


Figure 7. Understory vegetation abundance in hardwood stands in the western hemlock forests (WHS) at Nooksack (A) and thinned and unthinned stands in the WHS at Nooksack, Willapa Hills, and Springfield study areas (B) in western Oregon and Washington, 2000–2002. The right panel presents the mean for thinned and unthinned stands (± 1 SE) for each study area.

Table 3. Abundance (kg/ha) of plant life-form groups in commercially thinned and unthinned stands in the western hemlock (WHS) and Pacific silver fir (PSS) habitats in western Oregon and Washington, 2000–2002. Thinned-unthinned pairs within study areas flagged with A and B differed significantly at $0.05 < P < 0.10$ and those with C and D at $P \leq 0.05$. Forest ferns exclude bracken fern.

Study area ^a	Habitat	Thinned	n	Total		Conifers		Evergreen shrubs		Deciduous shrubs		Forbs		Graminoids		Forest ferns	
				\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Nk	WHS	No	16	392.9A	89.3	9.8	5.0	85.6	55.1	59.7C	26.6	1.9	0.9	0.4C	0.3	234.1	72.8
		Yes	17	642.1B	85.1	12.4	10.3	27.7	14.5	192.2D	47.0	9.6	3.5	4.1D	1.5	388.7	70.0
WH	WHS	No	31	278.3C	74.9	12.8C	5.4	34.0	9.6	17.0	5.7	9.8C	3.9	1.0C	0.4	203.3	68.0
		Yes	11	702.9D	155.2	67.1D	42.8	131.5	42.0	46.7	11.9	25.2D	13.1	8.9D	3.3	419.0	141.1
Sp	WHS	No	33	471.3	72.3	14.4	6.2	298.9	61.3	24.7	5.2	4.9A	1.2	0.4C	0.2	123.0	31.2
		Yes	7	439.8	92.3	35.0	21.1	260.4	44.6	68.6	45.3	19.6B	9.9	6.9D	4.1	47.0	10.9
Nk	PSS	No	9	312.2	161.4	189.9	143.2	41.1	40.9	46.1	21.4	13.4	6.6	0.4	0.2	11.0	4.1
		Yes	5	668.0	351.2	472.3	331.6	0.1	0.1	112.0	54.3	36.2	15.1	11.0	6.8	36.4	14.6

^a Study area codes are: Nk = Nooksack; WH = Willapa Hills; Sp = Springfield.

Several general trends in composition of plant life-form groups were evident in the WHS (Appendix D). Forbs and graminoids were well represented only during the first 10–15 years after logging disturbance. Deciduous shrubs also typically were well represented, whereas evergreen shrubs and forest ferns (mostly swordfern) were relatively uncommon in this early period.

Conifer biomass was minor the first 5 years, but increased rapidly and was variable thereafter. After about age 15, plant communities were strongly dominated by evergreen shrubs in the WHS-salal type, and forest ferns in the WHS-swordfern type (Appendix D). Similarly, graminoids, forbs, and deciduous shrubs were abundant only during the first 15 years in the PSS.

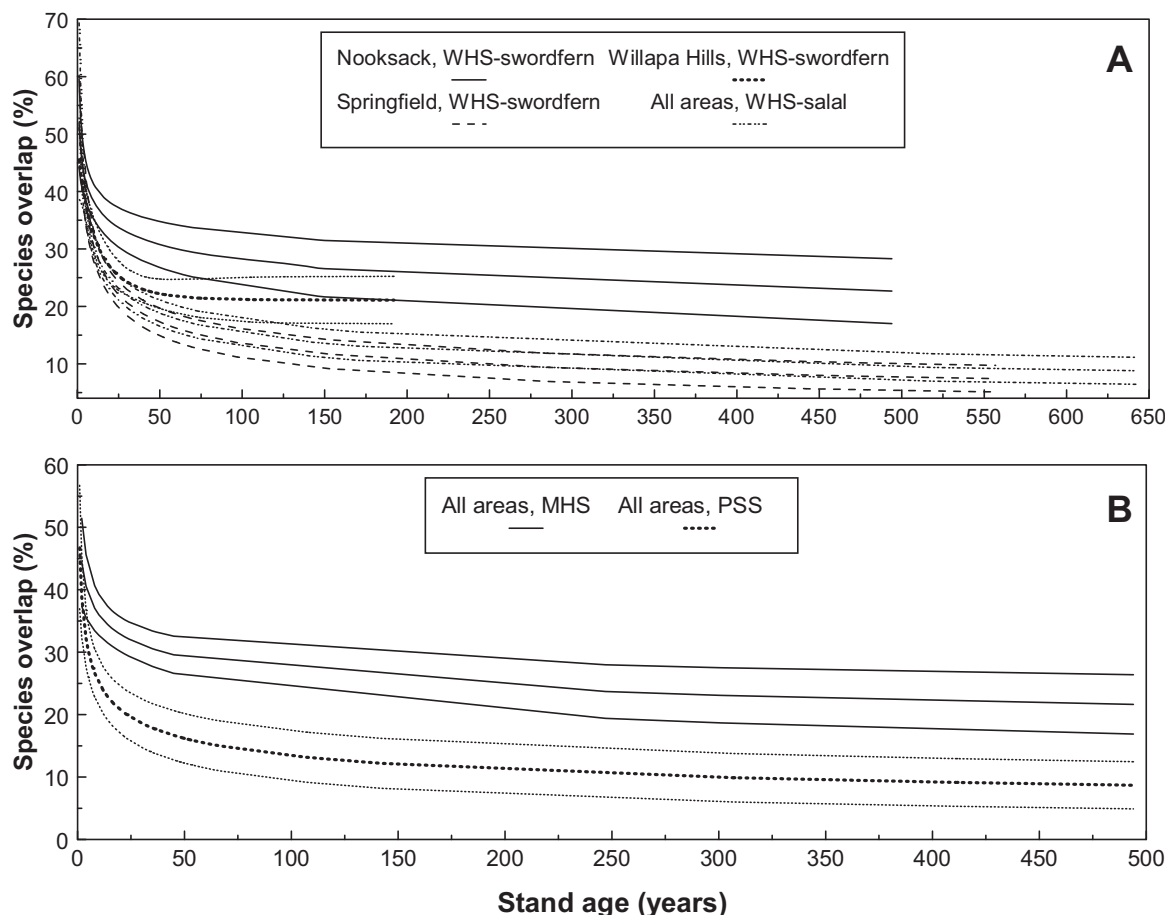


Figure 8. Community-wide overlap of plant species based on Kulczynski's similarity index (with 95% CI) across succession in the western hemlock (WHS)-swordfern habitat type at Nooksack, Willapa Hills, and Springfield study areas, the western hemlock (WHS)-salal habitat type combined across the 3 study areas (A); and the Pacific silver fir (PSS) and mountain hemlock series (MHS) combined across study areas (B) in western Oregon and Washington, 2000–2002. We calculated mean community composition for each species the first 4 years post-disturbance, and changes subsequently were based on differences in composition compared to these means. Graphs exclude data from thinned stands.

Thereafter, composition was variable, but conifers, evergreen shrubs, or forest ferns typically dominated. In the MHS, conifers dominated in the understory across all successional stages except in the first half-decade after stand initiation, and deciduous shrubs were well represented but subdominant to conifers throughout most stages. Forbs and graminoids were rare or virtually absent across all stages. In hardwood stands, understory composition exhibited little evidence of trends during the limited window of our samples. Forest ferns, forbs, and deciduous shrubs composed the majority of understory vegetation, and graminoids were well represented in most of these stands (Appendix D).

Abundance of most plant life-form groups was higher in thinned versus unthinned stands (Table 3). In the WHS, conifers, deciduous shrubs, forbs, and graminoids were more abundant ($P < 0.030$; no thinning \times study area interaction was significant for any plant group, $P > 0.06$). In the PSS, abundance of plant groups did not differ between thinned and unthinned stands, although abundance of conifers, deciduous shrubs, forbs, graminoids, and forest ferns each tended to be higher in thinned stands (Table 3).

Forage quality development.—We collected 1,071 plant samples from 232 macroplots ($n = 111, 63$, and 58 at Nooksack, Willapa Hills, and Springfield) for forage quality assays. With such a large sample size, all main effects (i.e., study area, habitat type, plant group, and season) and most 2-way interactions were highly significant ($P < 0.01$) despite very small differences in DE in many cases. The most prominent patterns were higher levels of DE in graminoids, forbs, and deciduous shrubs versus evergreen shrubs and forest ferns (2.67, 2.66, 2.60 vs. 2.09, and 1.93 kcal/g, respectively); higher DE in the PSS and MHS (combined) versus the WHS (2.82 vs. 2.63, 2.79 vs. 2.62, 2.60 vs. 2.60, 2.40 vs. 2.04, and 2.26 vs. 1.84 kcal/g for graminoids, forbs, deciduous shrubs, evergreen shrubs, and forest ferns); and higher DE in summer versus autumn (2.73 vs. 2.48, 2.71 vs. 2.49, 2.61 vs. 2.58, 2.12 vs. 2.00, and 1.94 vs. 1.93 kcal/g for graminoids, forbs, deciduous shrubs, evergreen shrubs, and forest fern), with seasonal changes more pronounced in herbs than shrubs and forest ferns.

Digestible energy of graminoids and forbs varied little with overstory canopy cover (Figs. 9 and 10). In contrast, DE of ferns, deciduous shrubs, and evergreen shrubs declined with increasing overstory canopy cover. However, it is unclear if DE declines were due to overstory development *per se* or simply due to changing species composition.

Community-wide successional profiles of forage DE suggested generally consistent differences over time by habitat types and seasons (Fig. 11). A prominent pattern was relatively high forage DE early in succession, and substantial declines after the first 10 years of succession in the WHS (Fig. 11A) at all study areas and after the first 30–40 years of succession in the PSS and MHS (Fig. 11C). In late succession, DE levels were variable, particularly in the WHS, but exhibited little evidence of increases. They were generally higher in the PSS and MHS than in the WHS across all stages of succession, and in summer versus autumn (Fig. 11B). These successional trends in DE were primarily driven by the shift from shade-intolerant deciduous shrubs, forbs, and graminoids, which were the plant groups with the highest DE levels, to shade-tolerant ferns and evergreen

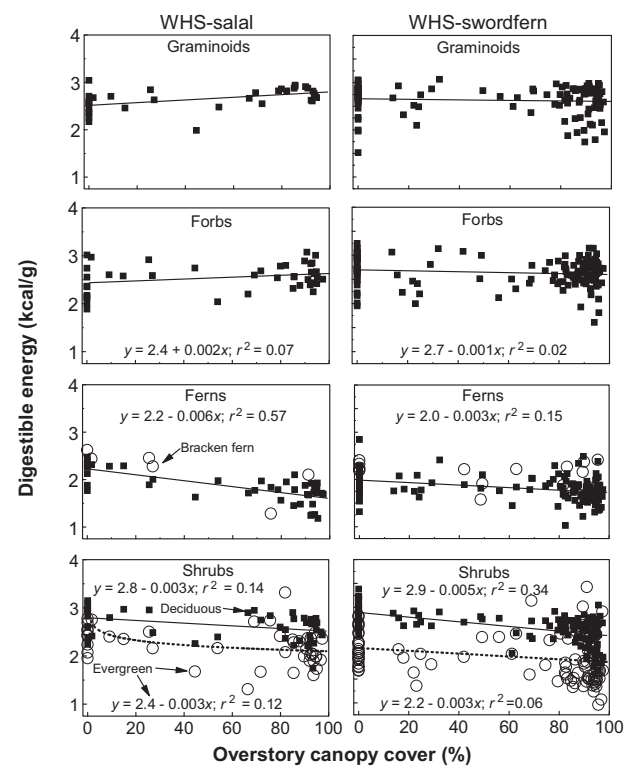


Figure 9. Relationships between digestible energy content of 5 plant groups and overstory canopy cover in the western hemlock (WHS)-salal and WHS-swordfern habitat types at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. We present regression equations and coefficients of determination for those plant groups that exhibited significant ($P \leq 0.05$) relations between digestible energy and canopy cover.

shrubs, which were the groups with the lowest DE levels, as succession advanced.

Community-wide DE was generally deficient for lactating elk in summer except during the first 10–12 years in the WHS and the first 35 years in the PSS and MHS (Fig. 11). Moreover, abundance of understory vegetation partitioned among our 4 forage DE value categories (poor to excellent) varied markedly across succession, habitat types, and seasons (Fig. 12). Vegetation of good and excellent quality was limited to stands < 15 years in age in the WHS, even in summer. After the first 15 years, nearly all vegetation was in the poor class in summer and early autumn. In the PSS and MHS, good and excellent forage persisted longer and was moderately more abundant in stands up to about 30 years after stand initiation, but good and excellent forage largely disappeared thereafter, particularly in autumn.

Overall, thinning had little effect on DE of individual plant groups or community-wide in the WHS. Initial analyses indicated a main effect of study area (higher at Nooksack; $P = 0.005$). With study area, thinning, and the thinning \times study area interaction in the ANOVA, neither of the latter 2 terms were significant for either community-wide DE levels or DE levels of any of the individual plant groups ($P > 0.19$). Community-wide DE levels in thinned plots were 1.94 ± 0.09 kcal (\pm SE) and 2.01 ± 0.07 kcal/g in the unthinned plots.

For the PSS, 6 unthinned macroplots and 5 thinned macroplots provided limited opportunity for comparison. However, com-

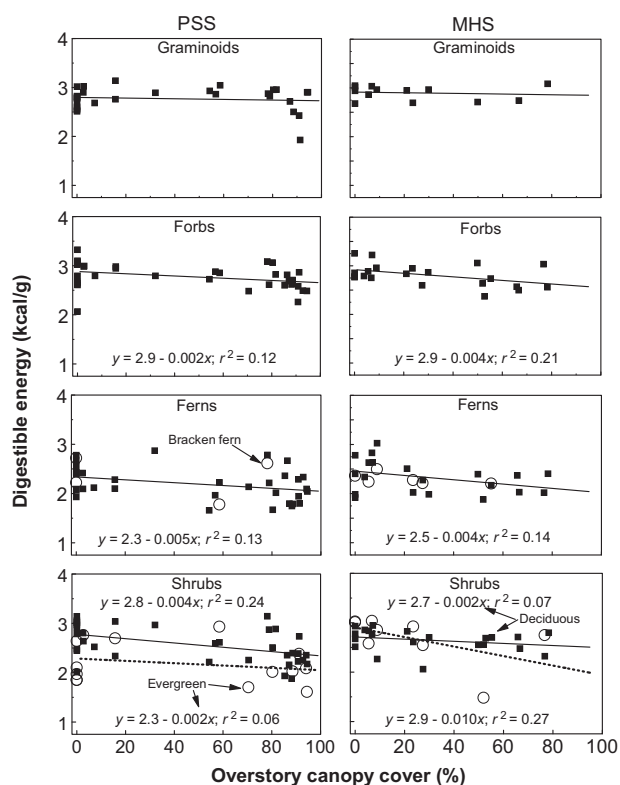


Figure 10. Relationships between digestible energy content of 5 plant groups and overstory canopy cover in the Pacific silver fir series (PSS) and mountain hemlock series (MHS) habitat types at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. We present regression equations and coefficients of determination for those plant groups that exhibited significant ($P \leq 0.05$) relations between digestible energy and canopy cover.

munity-wide forage DE levels were greater in thinned ($P = 0.022$) than in unthinned stands, and DE of deciduous shrubs was higher ($P < 0.001$) in thinned (2.89 ± 0.09) versus unthinned ($2.26 \text{ kcal/g} \pm 0.09$) stands. Digestible energy content of plant groups was otherwise invariant to thinning ($P > 0.15$ for evergreen shrubs, ferns, forbs, and graminoids) in the PSS.

Foraging Experiments

We sampled 89 macroplots for foraging dynamics using our tame elk across the 3 study areas: 33 at Nooksack, 27 at Willapa Hills, and 29 at Springfield. The WHS-salal type was well represented only in the Springfield sample, and the PSS and MHS types were well represented only at Nooksack. The majority of thinned and hardwood macroplots also were located at Nooksack (Table 2).

A key assumption of much of our work was that foraging intensity was invariant to time of day. This assumption was verified: bite mass, bite rate, and per-minute forage intake did not vary among morning, mid-day, and evening ($P > 0.08$ for main effect of time of day and $P > 0.42$ for the time of day \times study area interaction). The variable with the greatest tendency to differ, intake rate ($P = 0.08$), differed by $< 1 \text{ g}$ of forage/minute intake among time periods.

Dietary composition and selection.—We derived estimates of elk diets from 215,000 individual bites recorded during 240 hours of foraging trials on the first day of pen occupancy. We recorded bites on about 225 of 255 plant species identified during the

3 years of this study, although only $< 10\%$ of these species composed $> 2\%$ of elk diets in each of our habitats (see Appendix E for Chesson and Ivlev selection indices for each plant species, and Appendix F for graphs of percent use and availability for those species composing $\geq 1\%$ of elk diets or community composition).

Across the 3 study areas, deciduous shrubs composed the greatest portion of elk diets in summer and autumn (Fig. 13A). Forbs composed the second most common plant group in diets, although declines were apparent in autumn. Graminoids composed moderate to low levels in elk diets, with ferns and evergreen shrubs usually $< 10\%$ of elk diets, although evergreen shrubs composed 26% of diets in autumn at Springfield. When elk ate evergreen shrubs, they typically focused on very new growth, flowers, or berries. Conifers represented $< 3\%$ of elk diets on average and usually only included Douglas fir.

We identified 42 plant species as selected (SelSpp), 48 as avoided (AvdSpp), and 116 that were neither selected nor avoided (NeuSpp; Appendix E). Results from our 2 analyses to determine selection were similar, with the parametric t -test and non-parametric sign rank tests differing for 14 species. Sample size was ≤ 6 in each case, and for each of the 14 species, our final determination was based on our anecdotal observations of elk foraging behavior. Of vascular species present in > 2 elk pens, 15 SelSpp were deciduous shrubs, 11 were forbs, 4 were graminoids, and 1 was an evergreen shrub, whereas no ferns or conifers were selected by elk. All conifers, nearly all evergreen shrubs, most ferns, and some herbs were classed as AvdSpp. Graminoids and some species of deciduous shrubs and forbs were classed as NeuSpp (Appendix E).

Elk often consumed only small amounts of plant species that were abundant or dominant, such as salal, swordfern, Oregon grape, and trailing blackberry (Appendix E, F). In contrast, several species usually composed important portions of elk diets despite, in some cases, low relative abundance. These included red bilberry (*Vaccinium parvifolium*), vine maple (*Acer circinatum*), beadruby (*Maianthemum dilatatum*), devil's club (*Oplopanax horridum*), queen's cup beadlily (*Clintonia uniflora*), and mountain-ash. For non-vascular species, our observations were that elk virtually always consumed mushrooms whenever encountered, typically ate arboreal hair lichens (*Bryoria* spp.) when encountered, sometimes ate attached leaf lichens and other fungi (mainly conks of various species) when encountered, and rarely ate moss, despite its relative ubiquity in forested pens.

Selection patterns of plant life-form groups generally reflected selection of individual species; elk selected deciduous shrubs and avoided conifers, ferns, and evergreen shrubs (Fig. 13B). However, elk exhibited considerable variation in selection for individual taxa within deciduous shrubs, forbs, and graminoid groups, accounting for relatively weak selection of these plant groups overall. Elk were largely consistent in their avoidance of conifers, evergreen shrubs, and ferns. We found no evidence of a 3-way interaction of season \times study area \times plant group ($P = 0.49$) nor a 2-way interaction of season \times plant group on Ivlev index for plant groups ($P = 0.30$), whereas the study area \times plant group interaction was significant ($P < 0.001$). Evergreen shrubs (Ivlev index = -0.499), conifers (-0.484), and ferns (-0.455) were avoided, deciduous shrubs were selected (0.158), and grasses

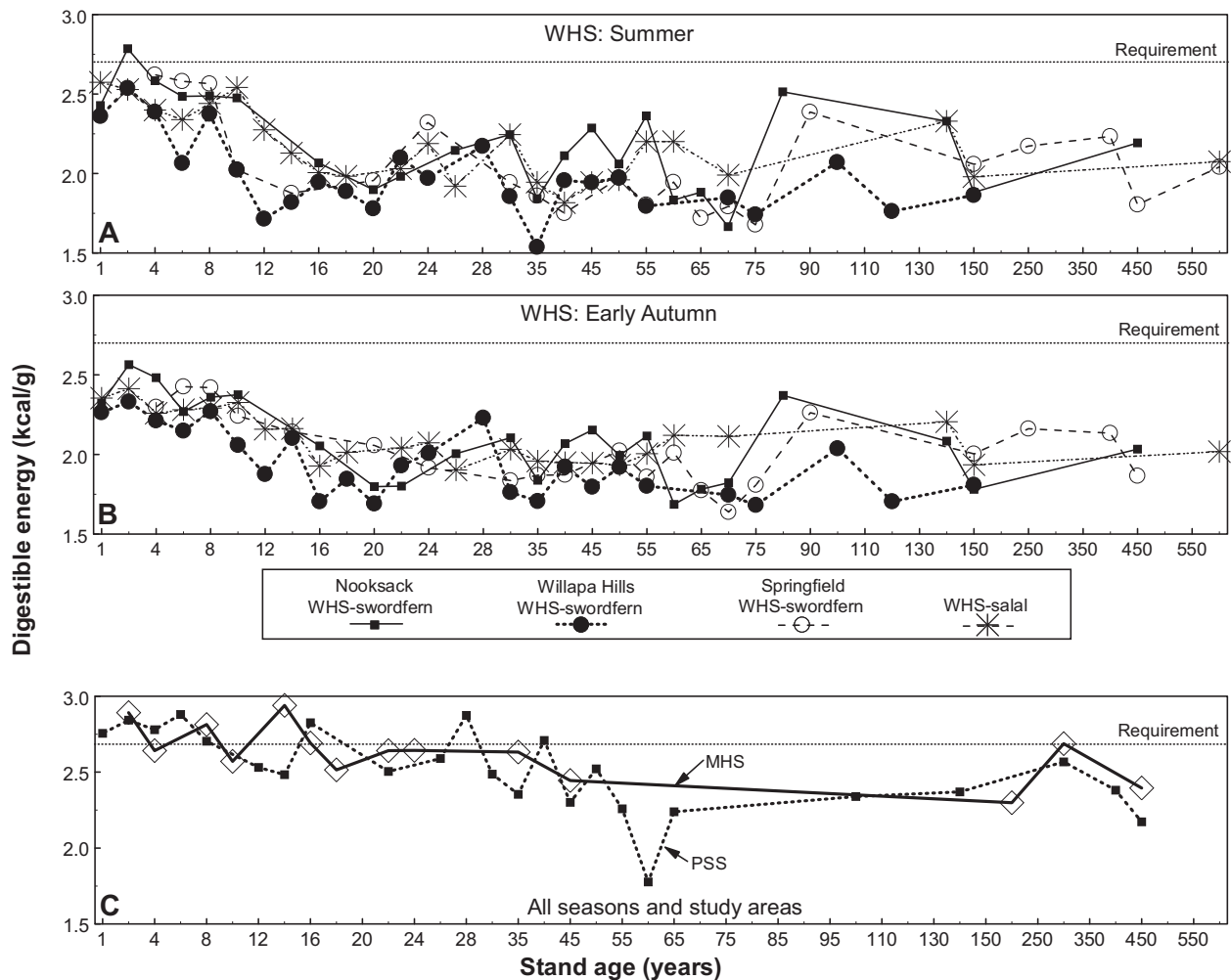


Figure 11. Community-wide forage digestible energy (DE) levels during succession (i.e., stand age) in the western hemlock series (WHS)–salal, WHS–swordfern, Pacific silver fir series (PSS), and mountain hemlock series (MHS) habitat types at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. In A and B, data are for the WHS–swordfern habitat type at each of the 3 study areas and pooled among study areas for the WHS–salal habitat type. In C, data for the PSS and MHS are pooled among seasons and study areas. Summer requirement indicated by the horizontal line in each panel is the level of DE in forage required by lactating elk to hold constant body fat levels in summer.

(0.079) and forbs (0.008) were consumed in proportions equal to their availability. Elk exhibited stronger avoidance of conifers and evergreen shrubs at Nooksack than at the other 2 study areas, and they avoided ferns more at Nooksack than at Springfield, based on least-squares means results (Fig. 13B).

For the 56 species that either composed >1% of community composition or >1% of elk diets, selected species were 4.5 times more abundant in diets than AvdSpp, yet AvdSpp were 10 times more abundant in plant communities than SelSpp, indicating that elk were avoiding many of the species most available to them. Additionally, bite mass of SelSpp averaged just 65% of bite mass of AvdSpp (Table 4), indicating that smaller bite mass of selected species failed to deter elk from seeking these plants. In contrast, DE levels evidently accounted for differences in selection; DE levels in evergreen shrubs and ferns, consistently avoided species, were significantly lower than the other forage classes, well below requirements of lactating elk.

Finally, abundance of each selection category varied across succession (Fig. 14) that strongly mirrored trends in abundance

by DE adequacy categories (Fig. 12). In the WHS, abundance of AccSpp species ranged from 200–600 kg/ha during the first 10 years of succession, but generally disappeared from plant communities thereafter. In the PSS and MHS, abundance of AccSpp ranged from 300–900 kg/ha during the first 30 years and thereafter largely disappeared from plant communities (Fig. 14; Appendix G).

Foraging dynamics.—We obtained usable actiwatch data from 35 pens: 19 of 29 pens at Willapa Hills and 16 of 33 pens at Nooksack. We had replicates (i.e., 2 elk with actiwatchers in the same pen) in 9 pens at Willapa Hills. Correct classification accuracy of our 3 activity categories was generally $\geq 90\%$, and predicted and observed time spent foraging was similar (usually $\pm 2\%$) in nearly all pens. Elk spent 3- to 4-fold more time foraging during the day than night, although this difference waned as daylength declined (Fig. 15). They averaged about 11.5 hours foraging in summer and 10.5 hours in early autumn (range: 7.9–15 hr) per day, or 55–60% of daylight hours and 33–42% of the night. From direct observations, percent of time

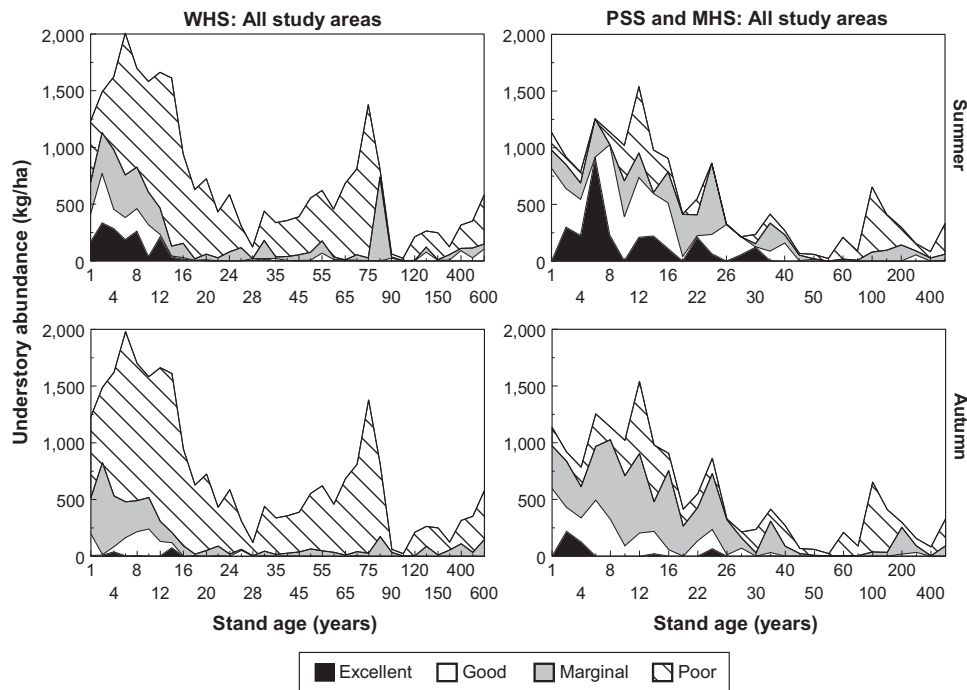


Figure 12. Abundance of understory vegetation by nutritional value category in the western hemlock (WHS), Pacific silver fir (PSS), and mountain hemlock series (MHS; with PSS and MHS combined) habitat types in western Oregon and Washington during summer and early autumn, 2000–2002. Nutritional categories (Cook et al. 2004) include excellent = digestible energy (DE) levels of >2.9 kcal/g and exceed nutritional needs of lactating elk and their calves; good = 2.75–2.9 kcal/g and impose only slight nutritional limitations; marginal = 2.40–2.75 kcal/g and may impose important reductions in nutritional condition and reproduction; and poor = <2.40 kcal/g and strongly affect nutritional condition and reproduction and may reduce survival probability.

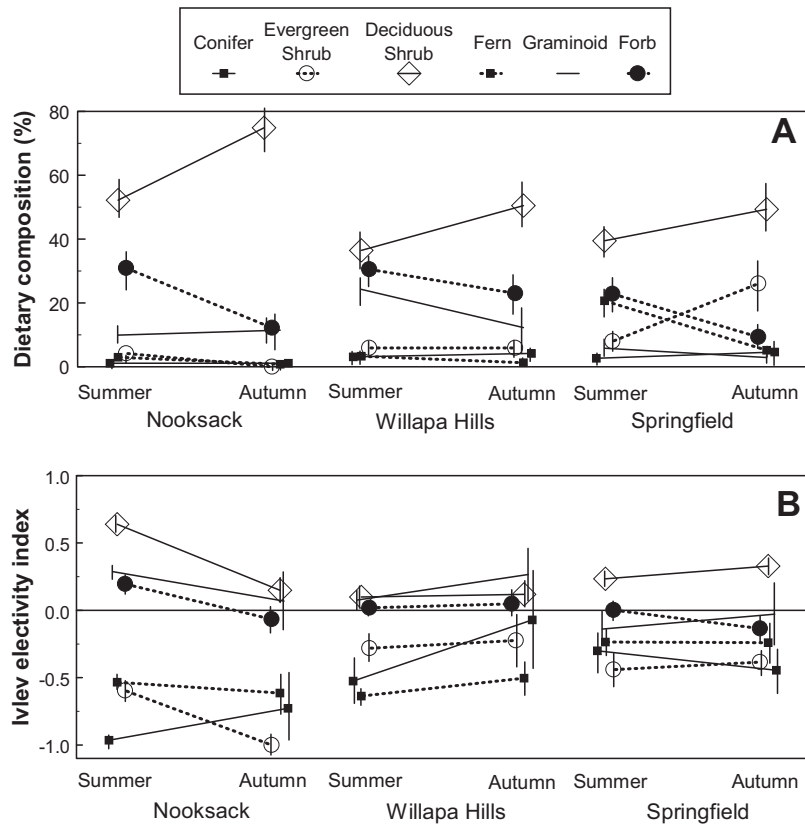


Figure 13. Dietary composition (A) and Ivlev electivity index (B) of plant life-form groups of elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Summer = late June to 15 September; Autumn = 15 September to early November. Vertical bars denote ± 1 standard error.

feeding averaged 55% (range: 38–78%), ruminating averaged 25% (range: 15–37%), inactive averaged 18% (range: 4–45%), and traveling averaged 3% (range: 1–18%) of daylight hours. Feeding + ruminating averaged 78% (range: 52–95%) of daylight hours.

Time spent feeding, ruminating, and feeding + ruminating during daylight hours and 24-hour periods generally did not vary as a function of study area, thinning treatment, habitat type, or successional stage, although a weak trend existed for elk to feed more in closed-canopy forests than in early seral stands during 24-hour periods (Table 5). Elk increased time feeding as canopy cover and stand age increased, a pattern that was moderately more pronounced for 24-hour periods versus daylight hours (Fig. 16). Feeding and feeding + ruminating during daylight hours and feeding during 24-hour periods peaked in August and September (Fig. 16).

Feeding time during daylight hours was unrelated to abundance of AvdSpp, NeuSpp, SelSpp, or AllSpp, but feeding time during 24-hour periods declined with increasing abundance of AvdSpp and AllSpp (Table 5; Fig. 17), a relation that was even stronger at night only (Fig. 17). Feeding time was uninfluenced by forage quality (i.e., mean forage DE of pens, DE-GFS, or the interaction of DE-GFS \times abundance of AccSpp; $P > 0.75$) or dietary DE or DP ($P > 0.22$). Dietary DE and 24-hour feeding time, however, were linearly related ($P = 0.030$) in the overall ANCOVA ($P = 0.005$), although we found no such influences of dietary DP (Fig. 18).

Rumination time increased with abundance of NeuSpp and declined with SelSpp ($P = 0.067$; Table 5), declined with increasing DE-GFS ($P = 0.058$) and dietary DE ($P = 0.052$), and increased with dietary NDF ($P = 0.005$; $P > 0.15$ for dietary ADF and DP). Thus, elk increased rumination time as forage and dietary quality declined, although these relations were imprecise ($r^2 \leq 0.08$). Ruminating + feeding time during daylight hours was unrelated to any of our forage classes (Table 5), forage quality, or any dietary quality variables ($P > 0.45$).

Speed of travel while foraging was unrelated to study area, thinning, habitat type, or date but was greater in closed-canopy forests versus early seral stages and increased with canopy cover and stand age (Figs. 19–23; Table 6). Speed was nonlinearly

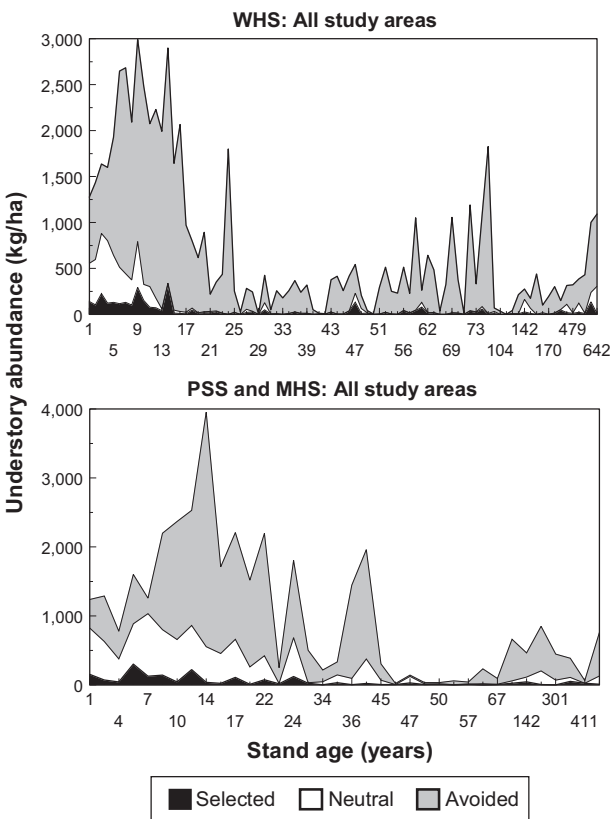


Figure 14. Abundance of understory vegetation by forage selection category in the western hemlock series (WHS) and Pacific silver fir (PSS) and mountain hemlock (MHS) series combined at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

related to abundance of AvdSpp and AllSpp, with higher rates of travel particularly at low levels of AvdSpp and AllSpp (Fig. 24). Elk also tended to increase speed at very high levels of biomass, if abundance of NeuSpp and SelSpp were relatively very low. In the 3 pens illustrating this pattern (Fig. 24), abundance of NeuSpp and SelSpp combined were $<10\%$ of total understory forage.

Bite mass was unrelated to thinning and date but was greater at Nooksack, in the WHS-salal and WHS-swordfern types, and in

Table 4. Dietary composition, abundance, and bite mass of 56 plant species by plant selection category (based on lvelev electivity index) and plant life-form group in western Oregon and Washington, 2000–2002. Replicates are the plant species using data only from elk pens in which the species was present (e.g., the 26 selected species separately averaged 5.85% of diets, 5.2 kg/ha in the pens, and 0.47 g/bite). Probability (P) values are for 1-way analyses of variance (ANOVAs) for each foraging variable within the plant group category; values with different letters among plant groups within a foraging variable and within a selection category differ ($P \leq 0.05$; $P < 0.1$ if marked with asterisk).

Plant group/type	<i>n</i> of species	Dietary composition (%)		Abundance (kg/ha)		Bite mass (g/bite)	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Selection category							
Selected	26	5.85A	0.946	5.2A	1.64	0.47A*	0.043
Neutral	15	3.62AB	0.633	10.4A	3.33	0.51AB*	0.081
Avoided	15	1.28B	0.575	53.2B	13.25	0.72B*	0.144
<i>P</i>		0.002		<0.001		0.096	
Plant life form							
Deciduous shrubs	21	5.36A*	1.114	9.1A	2.69	0.55AB	0.040
Evergreens ^a	11	1.44B*	0.774	66.2B	16.32	0.86A	0.178
Forbs	18	4.52A*	0.846	8.1A	2.68	0.37B	0.074
Graminoids	6	2.64AB*	0.391	3.8A	1.67	0.55AB	0.069
<i>P</i>		0.054		0.001		0.006	

^a Includes evergreen shrubs and evergreen ferns (swordfern and deer fern).

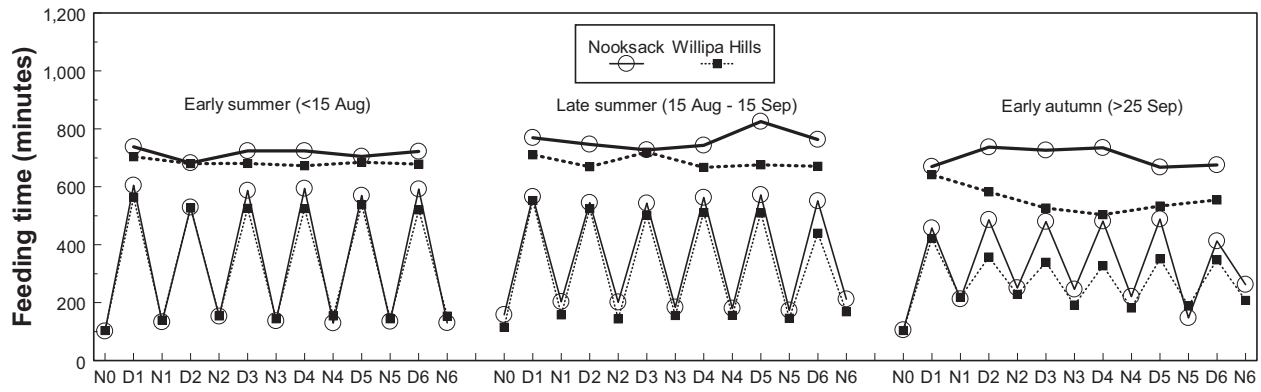


Figure 15. Feeding time of elk at Willapa Hills and Nooksack study areas, 2001–2002, in each day and night period of pen occupancy (D1–D6 = day 1–day 6; N1–N6 = night 1–night 6; N0 = first night elk were released into the pen and refers to the 6 hours prior to first light of D1). Lines above the day-night periods indicate total time spent feeding per 24 hours (SEs of means normally ranged from ± 15 –35 min and thus were too small to illustrate in this figure). We used only those data collected during the first 24 hours of pen occupancy, beginning the first morning, for analyses herein.

early seral versus closed-canopy forests (Figs. 19–20 and 23; Table 6). Bite mass increased across the early seral window and then declined as forest canopies closed and stand age increased (Figs. 21 and 22), was related to AvdSpp and NeuSpp and their

interaction, and was positively related to abundance of SelSpp and AllSpp (Fig. 25). The interaction suggested a complex relation; as abundance of NeuSpp declined, bite mass increased if AvdSpp was abundant, but bite mass declined as abundance of

Table 5. Initial analysis of covariance (ANCOVA) results for foraging and ruminating times of elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Covariates marked with an * or ** are significant at $0.05 < P \leq 0.10$ or $P \leq 0.05$, respectively.

Dependent variable ^a	<i>n</i>	<i>R</i> ²	<i>P</i>	Covariate of interest ^b	Covariates	Figure
Feed _{DLH}	72	0.09	0.408	SA	SA, HB _{WHS} *, TH, DT, CC	
Feed _{DLH}	52	0.07	0.753	TH	SA, HB _{WHS} , TH, DT	
Feed _{DLH}	84	0.10	0.380	HB _{All}	SA, HB _{All} , TH, DT, CC	
Feed _{DLH}	84	0.09	0.494	SUCC	SA, HB ₃ , SUCC, DT	
Feed _{DLH}	85	0.09	0.520	DT, CC	SA, HB _{All} , TH, DT, CC	16
Feed _{DLH}	84	0.09	0.520	AGE	SA, HB _{All} , TH, DT, AGE	16
Feed _{DLH}	86	0.04	0.764	FG	SA, DT, (A, N, S)	
Feed _{DLH}	86	0.02	0.828	FG	SA, DT, ALL	
Feed _{24-hr}	26	0.30	0.160	SA	SA, HB _{WHS} , TH, DT, CC*	
Feed _{24-hr}	24	0.13	0.394	TH	SA, TH, DT ^c	
Feed _{24-hr}	34	0.30	0.177	HB _{All}	SA, HB _{All} , TH, DT, CC	
Feed _{24-hr}	33	0.30	0.131	SUCC	SA, HB ₃ , SUCC*, DT*	
Feed _{24-hr}	34	0.30	0.177	DT, CC	SA, HB _{All} , TH, DT, CC**	16
Feed _{24-hr}	33	0.28	0.241	AGE	SA, HB _{All} , TH, DT*, AGE**	16
Feed _{24-hr}	35	0.32	0.036	FG	SA*, DT**, (A**, N*, S)	17
Feed _{24-hr}	35	0.27	0.019	FG	SA*, DT**, ALL**	17
Rum _{DLH}	72	0.05	0.796	SA	SA, HB _{WHS} , TH, DT, CC	
Rum _{DLH}	52	0.09	0.462	TH	SA, HB _{WHS} , TH, DT	
Rum _{DLH}	84	0.05	0.828	HB _{All}	SA, HB _{All} , TH, DT, CC	
Rum _{DLH}	84	0.05	0.836	SUCC	SA, HB ₃ , SUCC, DT	
Rum _{DLH}	85	0.06	0.737	DT, CC	SA, HB _{All} , TH, DT, CC	
Rum _{DLH}	84	0.08	0.611	AGE	SA, HB _{All} , TH, DT, AGE	
Rum _{DLH}	86	0.14	0.067	FG	SA, DT, (A, N*, S**)	
Rum _{DLH}	86	0.05	0.395	FG	SA, DT, ALL	
<i>F</i> + <i>R</i> _{DLH}	72	0.06	0.672	SA	SA, HB _{WHS} , TH, DT, CC	
<i>F</i> + <i>R</i> _{DLH}	52	0.01	0.990	TH	SA, HB _{WHS} , TH, DT	
<i>F</i> + <i>R</i> _{DLH}	85	0.07	0.720	HB _{All}	SA, HB _{All} , TH, DT, CC	
<i>F</i> + <i>R</i> _{DLH}	84	0.06	0.748	SUCC	SA, HB ₃ , SUCC, DT	
<i>F</i> + <i>R</i> _{DLH}	85	0.06	0.742	DT, CC	SA, HB _{All} , TH, DT, CC	
<i>F</i> + <i>R</i> _{DLH}	84	0.06	0.737	AGE	SA, HB _{All} , TH, DT, AGE	
<i>F</i> + <i>R</i> _{DLH}	86	0.08	0.526	FG	SA, DT, (A, N, N × SA*, S)	
<i>F</i> + <i>R</i> _{DLH}	86	0.01	0.930	FG	SA, DT, ALL	

^a Dependent variable codes are Feed_{DLH} = time (%) spent feeding during daylight hours; Feed_{24-hr} = time (%) spent feeding over 24-hour periods; Rum_{DLH} = time (%) ruminating during daylight hours; *F* + *R*_{DLH} = time (%) feeding and ruminating during daylight hours.

^b Covariate of interest was covariate for which the analysis was conducted; additional covariates were included to control for their effects. Covariate codes are SA = study area; HB_{WHS} = habitat types in the western hemlock series (WHS-salal and WHS-swordfern); HB₃ = includes Pacific silver fir series (PSS), mountain hemlock series (MHS), and both WHS combined; HB_{All} = all 4 habitat types; TH = thinned (yes or no); DT = date (month number + [day/31.1]); SUCC = successional stage (early seral or closed-canopy forest); CC = overstory canopy cover (%); AGE = stand age (years); FG = forage groups (kg/ha) and includes A = avoided species, N = neutral species, S = selected species, and ALL = all species.

^c HB_{WHS} dropped because no samples in the WHS-salal were available for this analysis.

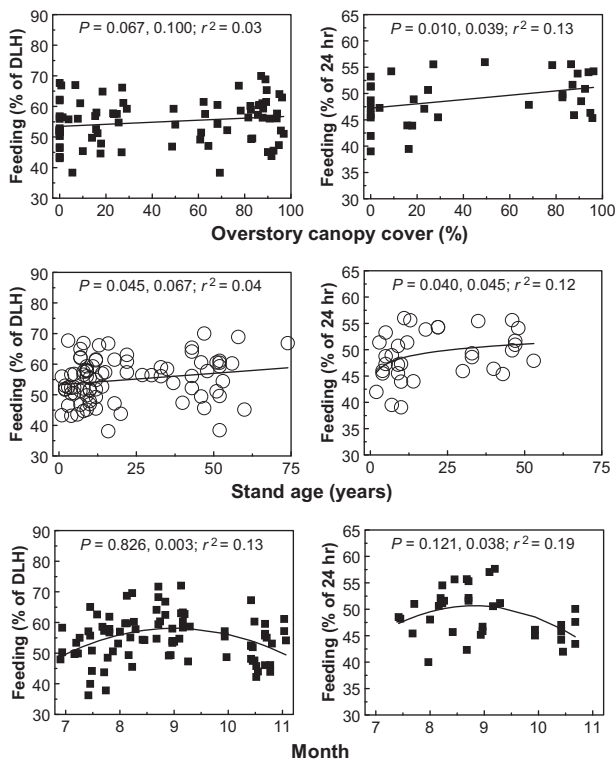


Figure 16. Percent of time elk spent feeding during daylight hours (DLH) and 24-hour periods at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002, in relation to canopy cover, stand age, and date. Within each graph, the first P value is for the covariate from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning treatment, date, and canopy cover or age, 1 ANCOVA per dependent variable (Table 5). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph calculated via linear or nonlinear regression techniques. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

NeuSpp declined if abundance of AvdSpp was low. Our interpretation is that elk consumed more AvdSpp, which generally afforded greater bite mass (Table 4), in pens with little NeuSpp and an abundance of AvdSpp.

Bites per minute was greater at Willapa Hills, in the MHS, in thinned stands, and early in summer but was unrelated to canopy cover or stand age (Figs. 19–23; Table 6). Bites per minute declined as abundance of AvdSpp and AllSpp increased (Fig. 26). Bites per minute has long been recognized to be inversely related to bite mass—the larger the bites, the slower herbivores eat because handling time increases (Wickstrom et al. 1984, Spalinger and Hobbs 1992), and it is possible that bite mass, and the vegetation attributes that affected bite mass, overrode those that affected bites per minute in our data sets. Thus, we reran the bites per minute ANCOVA with bite mass added to our covariates. Study area and date remained significant, whereas the forage classes were insignificant ($P > 0.43$), and we found an inverse, nonlinear relation between bites per minute and bite mass ($P < 0.001$). The negative relation between bite mass and bite rate existed in summer but not in autumn (Fig. 27) and suggested that bite mass set an upper limit

(see Wickstrom et al. 1984) on bite rate in summer but not in autumn.

Bites per meter traveled was greater at Willapa Hills, in the MHS, in early summer, and in early seral versus closed-canopy forests but was unrelated to thinning (Figs. 19 and 20; Table 6). It was linearly, inversely related to overstory canopy cover and stand age, and declined with date (Figs. 21–23; Table 6). Bites per meter traveled was unrelated linearly to our forage abundance variables, but weak, nonlinear relations with AvdSpp and AllSpp were evident (Fig. 26).

Forage intake per meter traveled was greater at Nooksack, in early seral versus closed-canopy forest, and in early summer but was unrelated to habitat type and thinning (Figs. 19, 20, and 23; Table 6). It was nonlinearly, inversely related to canopy cover and linearly, inversely related to stand age (Figs. 21 and 22; Table 6). As abundance of NeuSpp declined, so did intake rate if abundance of AvdSpp was low, but intake rate increased as NeuSpp declined if AvdSpp was relatively abundant (i.e., the same interaction involving bite mass; Fig. 28). Intake rate per meter increased as abundance of AllSpp increased, with some evidence of an inverted U-shaped relation as we found for bite rate per meter (Fig. 28; Table 6). Relations between forage intake per meter generally reflected that of bite mass, suggesting that bite mass largely was responsible for forage intake rate. Adding measures of forage DE to each of our foraging behavior ANCOVAs failed to identify significant contributions of these variables, with 1 exception: a positive, linear relation between bite mass and the DE-GFS \times AccSpp interaction ($P < 0.001$).

Many of the foraging behavior variables were potentially correlated, complicating interpretation of elk foraging strategies. We reran the ANCOVAs for each foraging behavior variable, sequentially including the other foraging behavior variables to derive a potentially more holistic interpretation of their foraging strategies. We found that when the speed ANCOVA included the quadratic terms AllSpp and AllSpp², speed while traveling was unrelated to any other of our measures of vegetative conditions, including forage DE levels, dietary DE and DP, habitat type, or study area or the other foraging behavior variables. Thus, we conclude that speed while foraging was primarily a function of AllSpp, with speed increasing markedly only when abundance of AllSpp was very low (< 500 kg/ha) and moderately when AllSpp was very high and abundance of SelSpp and NeuSpp was concurrently very low (Fig. 24). Bites per meter traveled, however, was influenced by date, speed of travel, and the interaction of speed \times bite mass (all inversely; $R^2 = 0.72$). Thus, bites per meter traveled was largely an emergent property directly influenced by speed, bite mass to a lesser degree, and date. In contrast, bites per minute was not influenced by speed of travel, suggesting that elk maintained biting rate per unit time by increasing their speed. Bites per minute was related only with bite mass, as noted above, and date, inversely for both covariates. Bite mass was high in plant communities that offered good nutritional value (high abundance of palatable and relatively nutritious forage) or, just the opposite, in plant communities that offered reduced opportunities for high-quality diets and high amounts of AvdSpp. Forage intake per meter was influenced by vegetation conditions affecting bite mass (NeuSpp, AvdSpp, AvdSpp \times NeuSpp but not with any of our measures of forage quality or

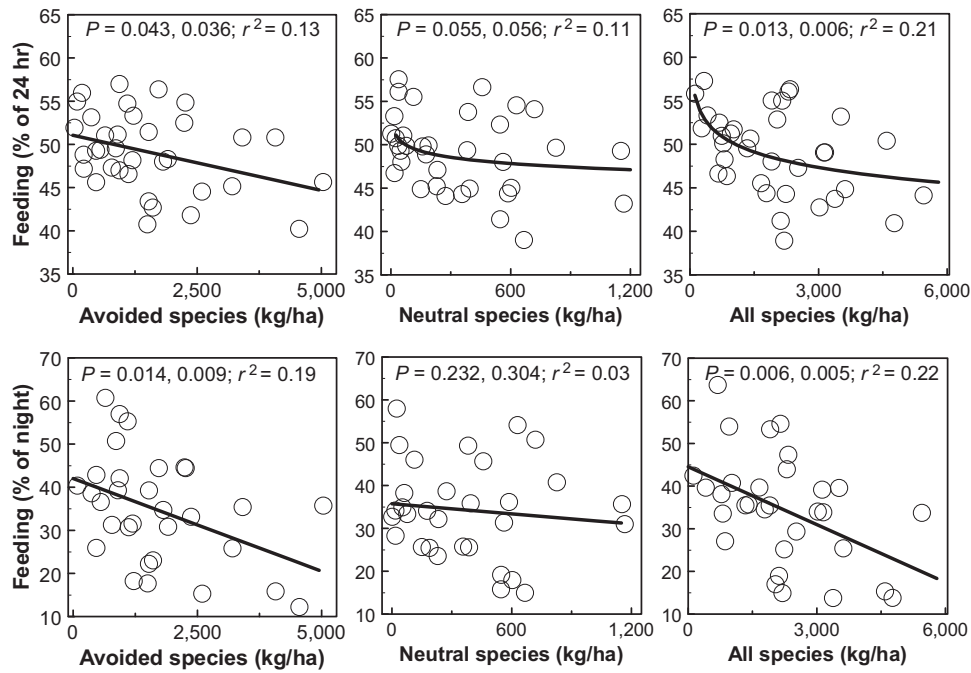


Figure 17. Percent of time elk spent feeding during 24-hour periods (top row) and at night (bottom row) at Nooksack and Willapa Hills study areas in western Oregon and Washington, 2001–2002, in relation to abundance of avoided plant species, neutral species, and total understory forage. We did not collect 24-hour and night data at Springfield. Within each graph, the first *P* value is from the overall analysis of covariance (ANCOVA) that included the forage covariates, study area, and date (Table 5), 1 ANCOVA per dependent variable. Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second *P* value and the *r*² are for the relation depicted in each graph calculated via linear or nonlinear regression techniques. The first *P* value is relevant if the relation is linear; the second *P* value is of interest if the relation is nonlinear.

dietary quality), date, and speed of travel. Switching to low-quality species offering high bite mass when palatable species were sparse helped maintained intake rate. Although formally evaluated below, forage intake per minute also was influenced by vegetation variables that influenced bite mass; speed was as unrelated to forage intake per minute as it was for bites per minute.

Nutrient content in elk diets.—We present data on dietary levels of tannin astringency, DMD, DE, crude protein, and DP.

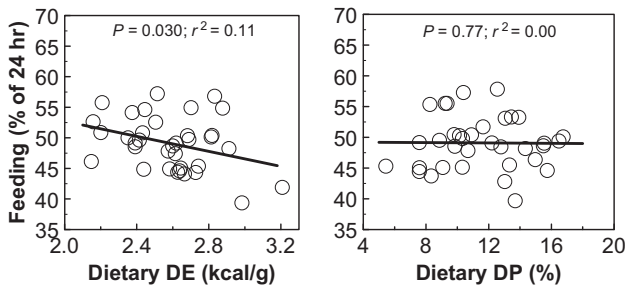


Figure 18. Percent of time elk spent feeding during 24-hour periods relative to digestible energy (DE) and digestible protein (DP) content of forage consumed at Nooksack and Willapa Hills study areas in western Oregon and Washington, 2001–2002. We did not collect 24-hour activity data at Springfield. The data are residuals, added to the overall mean of the dependent variable to rescale to the range of the original data, and were generated from analysis of covariance (ANCOVA) analyses that included study area, date, and abundance of all plant species (to account for these effects). We used the residuals to identify nonlinear relations. The *P* value was generated from the ANCOVA; the *r*² is for the depicted residuals.

Tannin astringency in elk diets was lowest at Willapa Hills but was otherwise unrelated to habitat type, thinning, or successional stage (Figs. 29 and 30; Table 7). However, we found nonlinear relations between tannin astringency and canopy cover and particularly stand age, where tannin astringency increased during the early seral period, then gradually declined as overstories developed (Figs. 31 and 32). No relationship with date was evident (Fig. 33). Tannin astringency increased weakly (*r*² ≤ 0.06) as abundance of AvdSpp increased and declined as NeuSpp increased (Fig. 34; Table 7). Because shading by overstories reduces tannin astringency (Van Horne et al. 1988, Happe et al. 1990), we ran the ANCOVA with canopy cover, canopy cover², NeuSpp, and the interaction of canopy cover × NeuSpp to evaluate the relative contribution of canopy cover versus plant species available on dietary tannin astringency. Including NeuSpp rendered both canopy cover terms insignificant (*P* > 0.11), whereas NeuSpp approached significance (*P* = 0.098) and study area remained the most important of the covariates (*P* = 0.004). These results suggest that composition of plants available to elk may influence dietary tannin astringency more than overstory canopy cover *per se*.

Dietary DE of 1 macroplot was highly anomalous and evidently unrepresentative of habitats in our study areas (e.g., located on a river terrace, soils mostly gravel, and plants phenologically advanced), and we eliminated this macroplot from analyses of dietary DMD, DE, and DP. Also, because DMD is a strong surrogate for DE and ANCOVA results were similar compared to those for DE, we presented means by study area and habitats (Figs. 29 and 30) but presented no additional results for DMD.

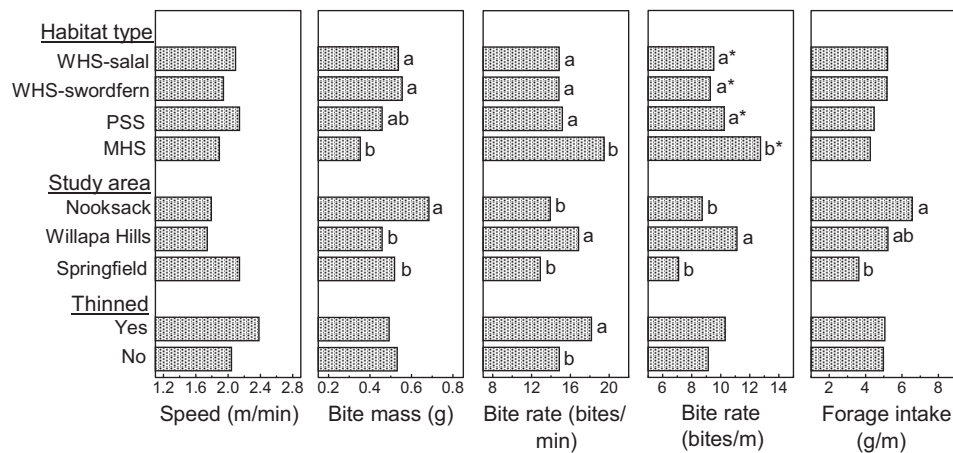


Figure 19. Foraging behavior of elk among 4 habitat types, between thinned and unthinned stands, and among the Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within factors (e.g., habitat type), horizontal bars with different letters differ significantly ($P \leq 0.05$; when letters have asterisks, then $0.05 < P \leq 0.10$). Habitat codes are WHS = western hemlock series; PSS = Pacific fir series; MHS = mountain hemlock series; WHS-salal and WHS-swordfern = 2 habitat types in the WHS. Effects of study area and thinning were based only on data from the WHS.

Dietary DE was greater at Nooksack, tended to be highest in the PSS and lowest in the WHS-salal habitat types ($P = 0.094$), and was greater in early seral stands (Figs. 29 and 30; Table 7). Dietary DE varied inversely with canopy cover and stand age, and tended to modestly decline with date ($P = 0.097$; Figs. 31–33; Table 7). Relations between dietary DE and NeuSpp and SelSpp were positive, whereas the coefficient of their interaction was negative (Fig. 35). This pattern suggested an alternative perspective, that the relation between abundance of NeuSpp and SelSpp with DE was nonlinear with an asymptote at relatively high levels of abundance, rather than an interaction between NeuSpp and SelSpp (Fig. 35).

Summing NeuSpp and SelSpp into AccSpp supported this alternative asymptotic interpretation, providing a simple, logical relation that indicated a threshold in AccSpp abundance below

which dietary DE declined substantially, and above which DE stabilized (the asymptote; Fig. 36). It also revealed an asymptote that was about 10% greater in the higher-elevation PSS and MHS versus the WHS (Fig. 36). Exponential equations fit for PSS and MHS combined were $DE = 0.92 \times (3.218 - e^{-0.0052(\text{AccSpp})})$ and separately for the WHS were $DE = 0.47 \times (5.755 - e^{-0.0041(\text{AccSpp})})$, where AccSpp is in kg/ha. Furthermore, the general nonlinear relation was consistent across season, habitat type, and study area (Fig. 37). Like bite mass, we expect that the declining DE levels resulted because elk switched from more palatable, nutritious forage to unpalatable forage offering lower DE levels as abundance of the more palatable species declined.

Estimates of dietary crude protein and DP were very highly correlated (Fig. 38A), and initial analyses with dietary crude

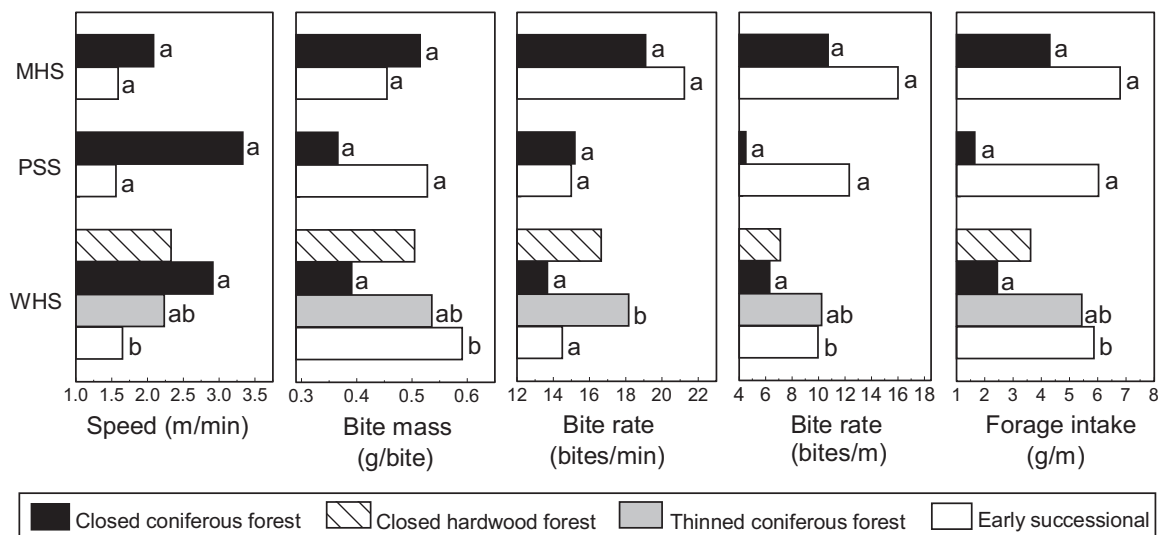


Figure 20. Foraging behavior of elk between early seral stages and closed-canopy forests in the western hemlock (WHS), Pacific silver fir (PSS), and mountain hemlock (MHS) habitat types and between thinned and unthinned coniferous forests in the WHS type at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. Data of hardwood forests ($n = 3$) are presented but were excluded from all analyses. Within forest series, bars with different letters differ significantly ($P \leq 0.05$). Relevant comparisons in the WHS are between early successional stands versus thinned and versus closed coniferous forests; appropriate results for thinning effects (thinned forests vs. unthinned forests across the same range of stand age) are in Fig. 19.

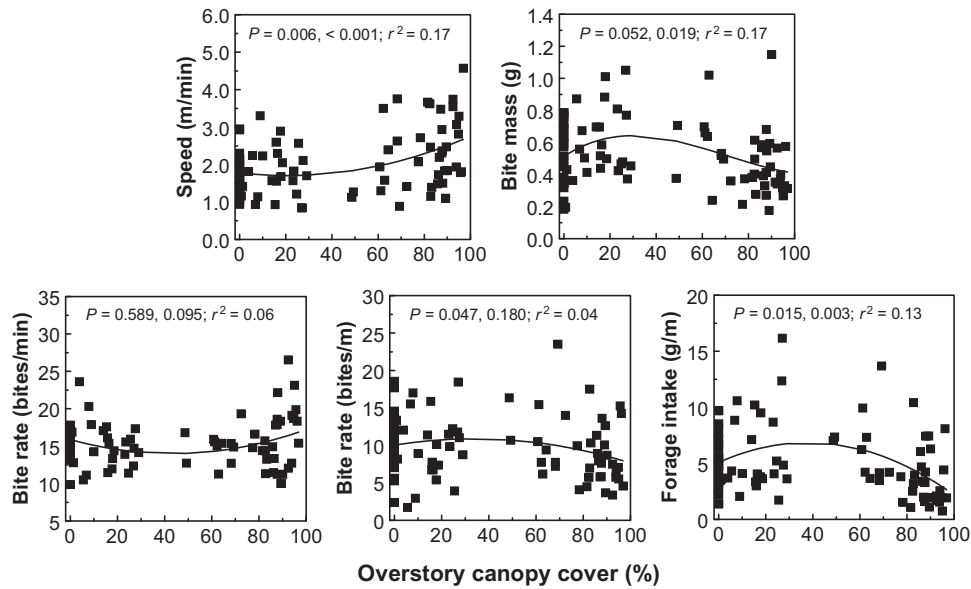


Figure 21. Foraging behavior of elk in relation to overstory canopy cover at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 6). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

protein indicated synonymous results with those of dietary DP, so we reported results only for DP, the more biologically relevant of the 2. In contrast, dietary DP was virtually unrelated to dietary DE (Fig. 38B), suggesting potential for substantial differences in dietary DP-habitat relations versus those for dietary DE.

Dietary DP was greater at Nooksack than Springfield, in the PSS, in closed-canopy forests versus early seral stages, in

summer, and was positively related to canopy cover and stand age (Figs. 29–33; Table 7). It was related to AvdSpp and NeuSpp and their interaction and was nonlinearly related to AllSpp but was unrelated to SelSpp (Fig. 39; Table 7). The main and interactive effects of AvdSpp and NeuSpp on dietary DP, however, were markedly complex and seemingly illogical. Initial plots suggested a nonlinear relation (logarithmic) with AvdSpp. When combined

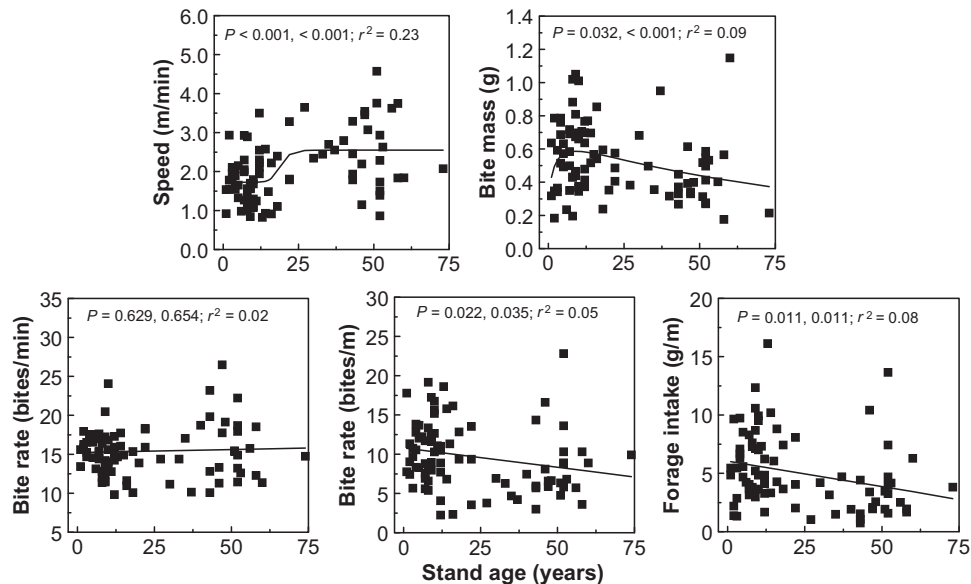


Figure 22. Foraging behavior of elk in relation to stand age at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and stand age (Table 6). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

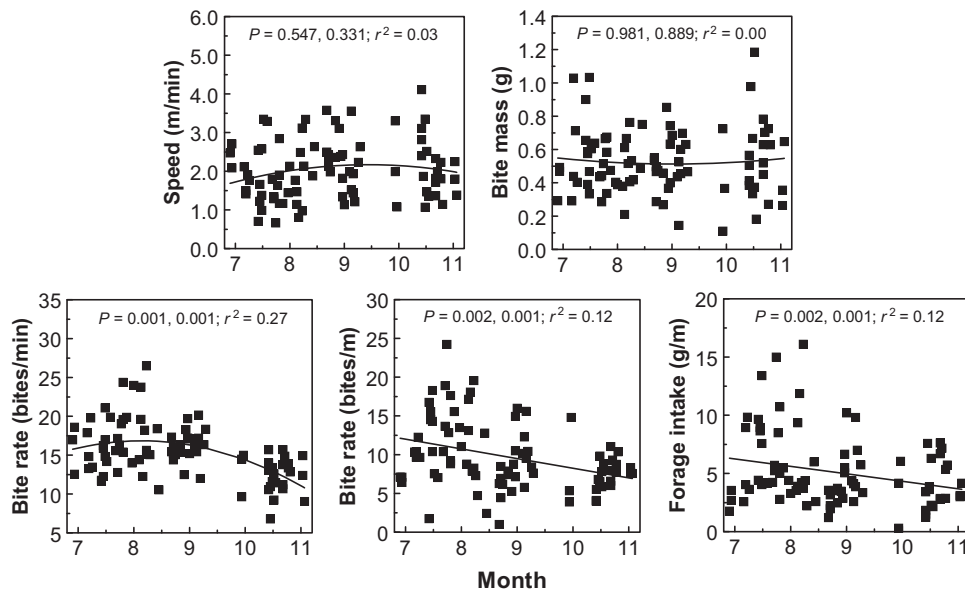


Figure 23. Foraging behavior of elk in relation to date at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 6). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

with the interactive influence of NeuSpp, the data suggested the pattern varied in relation to abundance of NeuSpp; DP declined as AvdSpp increased across low to moderate levels of AvdSpp but increased at higher levels of AvdSpp if abundance of NeuSpp was moderate to high (Fig. 39). Further, the interaction suggested DP increased with NeuSpp if AvdSpp was high, whereas DP declined with NeuSpp if AvdSpp was low (Fig. 39).

Our results from stepwise regression that included abundance of individual plant species provided markedly different insights that seemed more logical and holistic. Dietary DP varied significantly ($P < 0.025$) with salal (inverse, $r_p^2 = 0.20$), canopy cover (positive, $r_p^2 = 0.16$), lady-fern (positive, $r_p^2 = 0.09$), salmonberry (positive, $r_p^2 = 0.05$), red alder (positive, $r_p^2 = 0.05$), baldhip rose (*Rosa gymnocarpa*; inverse, $r_p^2 = 0.03$), date (inverse, $r_p^2 = 0.03$), and fireweed (inverse, $r_p^2 = 0.03$; r_p^2 = partial coefficient of determination). Salal dominates on dry sites in the WHS (Franklin and Dyrness 1988); lady-fern, salmonberry, and red alder occupy wetter forests, swamps, and streambanks (Pojar and MacKinnon 1994); red alder is a nitrogen-fixing species that enhances soil nitrogen (Tarrant and Miller 1963, Bormann and DeBell 1981); and fireweed is a common pioneering perennial forb abundant in early successional stages (we are unsure if baldhip rose is a relevant site indicator). Running the DP ANCOVA with the main effects of study area ($P = 0.008$), date ($P < 0.001$), salal ($P < 0.001$), lady-fern ($P = 0.001$), red alder ($P = 0.016$), salmonberry ($P = 0.067$), and fireweed ($P = 0.045$) provided a substantially higher coefficient of determination ($R^2 = 0.63$, $P < 0.001$) than did the DP ANCOVAs described above ($R^2 = 0.37 - 0.46$; Table 7). The correlations we observed indicated that elk acquired higher dietary DP relatively early in the summer-autumn season, on sites with relatively high soil moisture throughout most of the growing season, on sites with nitrogen-enhanced soils, and in stands with

moderately high canopy cover particularly if red alder was an important component of the overstory (Fig. 40). Dietary DP levels in our 6 alder-dominated hardwood stands exceeded those in the other habitats or successional stages (Fig. 30D), and most of these sites had wet soils in autumn when sampled. Probability of high dietary DP was low in WHS-salal types particularly where salal was abundant and canopy cover low (Fig. 40).

Dietary DE was positively related to DE-GFS ($P = 0.017$) and community-wide mean forage DE ($P < 0.001$) but was unrelated to the interaction of DE-GFS and abundance of AccSpp ($P = 0.19$). Dietary tannin astringency and DP were unrelated to any of our forage-quality measures ($P > 0.51$).

Intake rates.—Forage dry matter, DE, and DP per-minute intake rates in the WHS were greater at Nooksack compared to the other 2 study areas but were similar among habitat types. Intake rates of forage and DE were not influenced by thinning in the WHS, whereas intake rate of DP was greater in thinned versus unthinned stands (Fig. 41; Table 8). Forage and DE intake rates were lower in closed-canopy forests and were inversely related with stand age and overstory canopy, whereas DP intake rate varied little in relation to these measures of succession (Figs. 42–44; Table 8). Intake rates of forage, DE, and DP declined with date (Fig. 45; Table 8). Intake rates of forage, DE, and DP per 24 hours exhibited similar patterns as those on a per minute basis, but ANCOVAs were generally insignificant, reflecting the smaller sample size of 24-hour data. However, DP intake rate per 24 hours was significantly related to study area, thinning, and successional stage (Table 8; higher at Nooksack, in thinned forests vs. closed-conifer forests, and in thinned forests vs. early seral stages).

Patterns of forage intake per minute in relation to abundance of forage selection categories were complex, reflecting an interaction

Table 6. Initial analysis of covariance (ANCOVA) results for foraging behavior variables of elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Covariates marked with an * or ** are significant at $0.05 < P \leq 0.10$ or $P \leq 0.05$, respectively.

Dependent variable ^a	<i>n</i>	<i>R</i> ²	<i>P</i>	Covariate of interest ^b	Covariates	Figure
Speed	72	0.20	0.026	SA	SA, HB _{WHS} , TH, DT, CC**	19
Speed	53	0.13	0.239	TH	SA, HB _{WHS} , TH, DT	19
Speed	86	0.20	0.027	HB _{All}	SA, HB _{All} , TH, DT, CC**	19
Speed	86	0.18	0.026	SUCC	SA, HB ₃ , SUCC**, DT	20
Speed	86	0.20	0.023	DT, CC	SA**, HB _{All} , TH, DT, CC**	21, 23
Speed	85	0.21	0.015	AGE	SA*, HB _{All} , TH, DT, AGE**	22
Speed	89	0.22	0.002	FG	SA, DT, (A**, N, S)	24
Speed	89	0.23	<0.001	FG	SA, DT, ALL**	24
Bite mass	72	0.18	0.038	SA	SA**, HB _{WHS} , TH, DT, CC	19
Bite mass	53	0.21	0.037	TH	SA**, HB _{WHS} , TH, DT*	19
Bite mass	86	0.17	0.054	HB _{All}	SA**, HB _{All} **, TH, DT, CC*	19
Bite mass	86	0.19	0.018	SUCC	SA**, HB ₃ , SUCC**, DT	20
Bite mass	86	0.17	0.054	DT, CC	SA**, HB _{All} **, TH, DT, CC*	21, 23
Bite mass	85	0.19	0.048	AGE	SA**, HB _{All} **, TH, DT, AGE**	22
Bite mass	89	0.28	<0.001	FG	SA**, DT, (A**, N*, A × N**, S*)	25
Bite mass	89	0.13	0.018	FG	SA**, DT, ALL**	25
BR/min	72	0.51	<0.001	SA	SA**, HB _{WHS} , TH**, DT**, CC	19
BR/min	53	0.39	<0.001	TH	SA**, HB _{WHS} , TH**, DT**	19
BR/min	86	0.56	<0.001	HB _{All}	SA**, HB _{All} **, TH**, DT**, CC	19
BR/min	86	0.48	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT**	20
BR/min	86	0.56	<0.001	DT, CC	SA**, HB _{All} **, TH**, DT**, CC	21, 23
BR/min	85	0.55	<0.001	AGE	SA**, HB _{All} **, TH**, DT**, AGE	22
BR/min	89	0.35	<0.001	FG	SA**, DT**, (A**, N, S)	26
BR/min	89	0.34	<0.001	FG	SA**, DT**, ALL**	26
BR/m	72	0.38	<0.001	SA	SA**, HB _{WHS} , TH, DT**, CC*	19
BR/m	53	0.29	0.006	TH	SA**, HB _{WHS} , TH, DT**	19
BR/m	86	0.41	<0.001	HB _{All}	SA*, HB _{All} , TH, DT**, CC*	19
BR/m	86	0.38	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT**	20
BR/m	86	0.41	<0.001	DT, CC	SA**, HB _{All} , TH, DT**, CC**	21, 23
BR/m	85	0.42	<0.001	AGE	SA**, HB _{All} , TH, DT**, AGE**	22
BR/m	89	0.28	<0.001	FG	SA**, DT**, (A, N, S)	26
BR/m	89	0.28	<0.001	FG	SA**, DT**, ALL	26
Intake/m	72	0.25	0.004	SA	SA**, HB _{WHS} , TH, DT*, CC*	19
Intake/m	53	0.14	0.190	TH	SA, HB _{WHS} , TH, DT	19
Intake/m	86	0.25	0.003	HB _{All}	SA*, HB _{All} , TH, DT**, CC**	19
Intake/m	86	0.29	<0.001	SUCC	SA*, HB ₃ , SUCC**, DT**	20
Intake/m	86	0.26	0.002	DT, CC	SA**, HB _{All} , TH, DT**, CC**	21, 23
Intake/m	85	0.27	0.002	AGE	SA**, HB _{All} , TH, DT**, AGE**	22
Intake/m	89	0.36	<0.001	FG	SA**, DT**, (A**, N**, A × N**, S)	27
Intake/m	89	0.25	<0.001	FG	SA**, DT**, ALL**	27

^a Dependent variable codes are speed = m traveled/min while foraging; bite mass = mass of bites (g/bite); BR/min = bites/min; BR/m = bites/m; Intake/m = dry matter intake (g)/m traveled while foraging.

^b Covariate of interest was covariate for which the analysis was conducted; additional covariates were included to control for their effects. Covariate codes are SA = study area; HB_{WHS} = habitat types in the western hemlock series (WHS-salal and WHS-swordfern); HB₃ = includes Pacific silver fir series (PSS), mountain hemlock series (MHS), and both WHS combined; HB_{All} = all 4 habitat types; TH = thinned (yes or no); DT = date (month number + [day/31.1]); SUCC = successional stage (early seral or closed-canopy forest); CC = overstory canopy cover (%); AGE = stand age (years); FG = forage groups (kg/ha) and includes A = avoided species, N = neutral species, S = selected species, and ALL = all species.

of AvdSpp and NeuSpp (Fig. 46; Table 8). As abundance of NeuSpp declined, so too did forage intake rate if abundance of AvdSpp was low, but intake rate increased if AvdSpp was abundant. A nonlinear, hump-backed relation existed between AllSpp and forage intake rate per minute, suggesting depressed intake rate at very low and very high abundance of total forage.

Relations among DE intake per minute and abundance of forage selection categories were also complex, with all terms in the ANCOVA model significant, except AvdSpp, including the NeuSpp × AvdSpp and NeuSpp × SelSpp interaction (Table 8). Our usual residuals analyses failed to clarify relations between DE intake rate and forage abundances (hence, we did not present our usual graphs of DE intake with the forage selection groups). Returning to the original data, we plotted DE intake with

AccSpp by study area and by our high- and low-elevation habitat types as we did for dietary DE, and fit regressions by study area and by habitat types (Fig. 47). Several points seemed evident. First, relations between DE intake rate and AccSpp existed, but the nature of the relation was markedly different among study areas. In particular, DE intake at Springfield at low levels of AccSpp was comparatively very low (Fig. 47A). Second, with data pooled among study areas, little difference existed in DE intake rate between high- and low-elevation habitats. Third, in both analyses, an asymptotic relation between AccSpp and DE intake rate per minute was generally evident, with a threshold in DE intake rate at about 200 kg/ha of AccSpp (Fig. 47B). In contrast, intake rate per minute of DP was unrelated to abundance of the forage selection categories, except for a linear, inverse relation with NeuSpp ($r^2 = 0.07$; $P = 0.017$; Table 8).

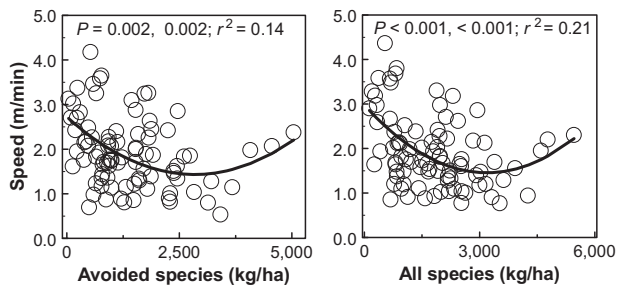


Figure 24. Speed of elk while foraging in relation to abundance of avoided and all forage species at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included independent variables study area, date, and the 3 forage groups or total forage (Table 6). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

Forage dry matter and DE intake per 24 hours were related to the $\text{AvdSpp} \times \text{NeuSpp}$ interaction (Figs. 48 and 49; Table 8), the same interaction evident for bite mass (Fig. 25) and per-minute intake rate of forage dry matter (Fig. 46). Intake rate of DP per 24 hours was weakly inversely related to abundance of AvdSpp , NeuSpp , and total forage, with no significant interaction between AvdSpp and NeuSpp (Fig. 50; Table 8). Adding our forage quality measures to the intake ANCOVAs indicated no improvement in the results. We found no significant relations between community-wide DE, DE-GFS, or the interaction of DE-GFS and AccSpp with any of our intake rate variables ($P > 0.11$).

The final step of our intake rate analysis was to evaluate the extent to which each of the 4 foundation variables (bite mass, bite rate, either dietary DE or DP, and foraging time) plus date and study area influenced estimates of intake rates of DM, DE, and DP per minute and 24-hour periods (the dependent variables). Neither study area nor date were significant ($P \geq 0.12$) in any of the 6 ANCOVAs. When we reran the analyses as regressions with study area and date excluded, bite mass contributed most to intake rate of forage dry matter and DE intake rates per minute

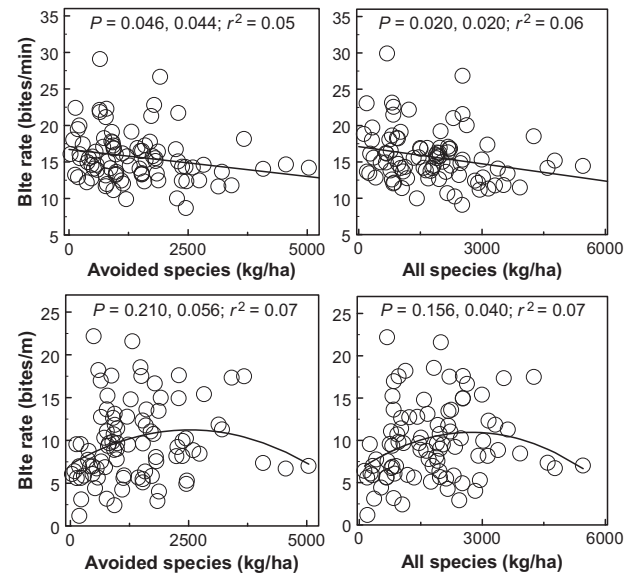


Figure 26. Bite rate per minute and per meter traveled of elk in relation to abundance of 3 forage types and total forage at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included independent variables study area, date, and the 3 forage groups or total forage (Table 6). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

and per 24 hours, and was second only to DP content of diets for estimates of DP intake per minute and per 24 hours. Bite rate per minute and time spent feeding each 24 hours had relatively small effects on estimates of intake rate (Table 9).

In sum, despite the complexity of relations between plant community attributes and nutrient intake, several simple patterns generally held in respect to seral stage, particularly in light of nutritional requirements of lactating elk in summer (Fig. 51). For dietary DE and DE intake rates, early successional and high-elevation habitats generally were superior. Intake of DE particularly was strongly inadequate in WHS habitats and in all habitats on a 24-hour basis for lactating females in summer.

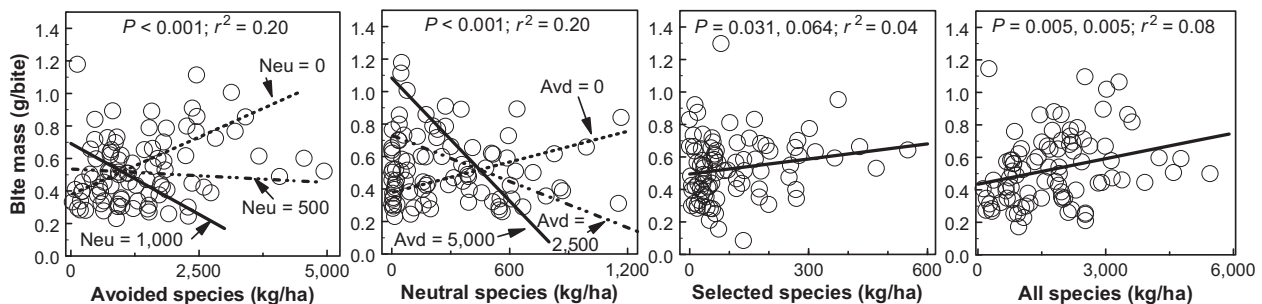


Figure 25. Bite mass of elk in relation to abundance of 3 forage types (avoided [avd], neutral [neu], selected) and total forage at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included independent variables study area, date, and the 3 forage groups or total forage (Table 6). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. For the avoided and neutral species graphs, the 3 regression lines illustrate the avoided \times neutral species interaction effect on bite mass. For the selected and all species graphs, the second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

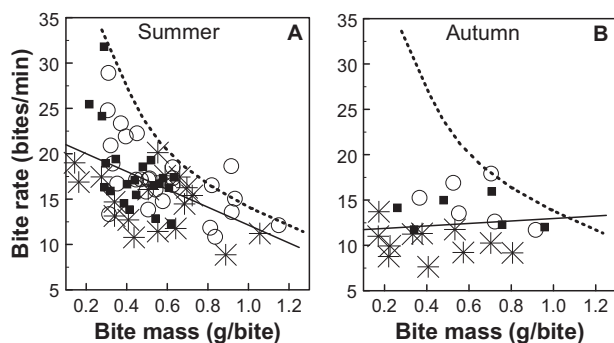


Figure 27. Relationship between bite rate and bite mass of elk in summer (A) and autumn (B) in western Oregon and Washington, 2000–2002. Data points indicated by open circles are from Nooksack, dark squares are from Willapa Hills, and asterisks are from the Springfield study area. The dotted curve was hand-fitted to illustrate a possible approximate maximum bite rate across different levels of bite mass.

Intake of DP was less influenced by successional stage, with the highest levels of DP occurring in thinned stands and alder-dominated hardwood stands (the latter usually with saturated soils). Finally, DP deficiencies were less pronounced than DE deficiencies, with some habitats supporting DP intake levels in excess of maintenance requirements (Fig. 51).

Our constraint for animal welfare of excluding potential pen sites with low abundance of forage is relevant in light of findings of nutritional value by seral stage (Fig. 51). In young seral stages, abundance of AccSpp was similar in sites with and without elk, 553 versus 603 kg/ha at Nooksack, 720 versus 430 kg/ha at Willapa Hills, and 371 versus 359 kg/ha at Springfield. However, abundance of AccSpp and AllSpp in closed-canopy forests was about twice that in macroplots with elk than in those without ($P < 0.001$; Fig. 52). Thus, we probably overestimated the nutritional value of closed-canopy forests (Fig. 51), particularly at Nooksack.

Foraging Experiments: Body Fat and Calf Growth

Early-summer levels of IFBF in adult females averaged 14.5% at Nooksack, 14% at Willapa Hills, and 9.8% at Springfield. Elk lost IFBF in each of the 15 trials conducted over the 3 years, and

averaged a decline of 0.1 percentage points of IFBF per day. In mid-September when elk were removed from the field enclosures for breeding, IFBF averaged 9.6% at Nooksack, 7.3% at Willapa Hills, and 5.9% at Springfield. Calf body mass averaged 36 kg, 46 kg, and 37 kg at the beginning of the summer trials and averaged at 74 kg, 83 kg, and 68.5 kg at the end of the trials in mid-September at Nooksack, Willapa Hills, and Springfield, respectively.

The trend in greater declines in IFBF at Willapa Hills and Springfield compared to Nooksack was not significant ($P > 0.35$; Fig. 53). Calves at Nooksack gained 50% more mass than did calves at Willapa Hills and Springfield, an effect that approached significance ($P = 0.10$ for the overall ANOVA; $P = 0.058$ for main effect of study area). We detected no significant effects of forest succession stage or habitat type for either IFBF change in adults or calf growth (Fig. 53).

Average dietary DE and DE intake per minute during the trials were linearly related to IFBF change, although intake rate of DE accounted for twice the variance of IFBF change compared to dietary DE (Fig. 54). We found no evidence that DP or DP intake influenced IFBF changes ($P > 0.63$). Abundance (kg/ha) of NeuSpp and AccSpp separately exhibited modest nonlinear relations with IFBF change. However, expressing these variables in kilograms per elk-day of use (a reflection of the total amount of forage in the pens rather than forage density) improved their relation with IFBF. The strongest relations between IFBF and forage abundance resulted from combining SelSpp and NeuSpp into AccSpp and, again, expressing the relation based on total AccSpp in the pens rather than density of AccSpp (kg/ha; Fig. 54).

Growth of calves was weakly linearly correlated with dietary DE and DP intake rate of their mothers (Fig. 55). Unlike IFBF change of their mothers, calf growth was not related to DE intake per minute of their mothers. However, removal of a relatively anomalous data point (Fig. 55) provided a linear regression that accounted for more variation ($r^2 = 0.28$) in calf growth than any other variables we examined. This pen was a mid seral, closed-canopy stand at Willapa Hills, with sporadic small patches of Oregon oxalis (*Oxalis oregana*), a palatable forb that evidently was too low in abundance to support high DE intake rate by adults

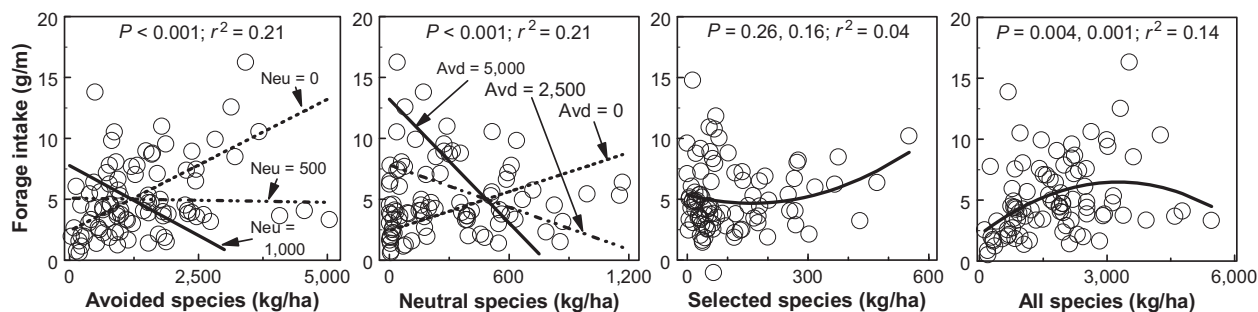


Figure 28. Forage intake rate per meter traveled of elk in relation to abundance of 3 forage types (avoided [avd], neutral [neu], selected) and total forage at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included independent variables study area, date, and the 3 forage groups or total forage (Table 6). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. For the avoided and neutral species graphs, the 3 regression lines illustrate the avoided \times neutral species interaction effect on forage intake rate. For the selected and all species graphs, the second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

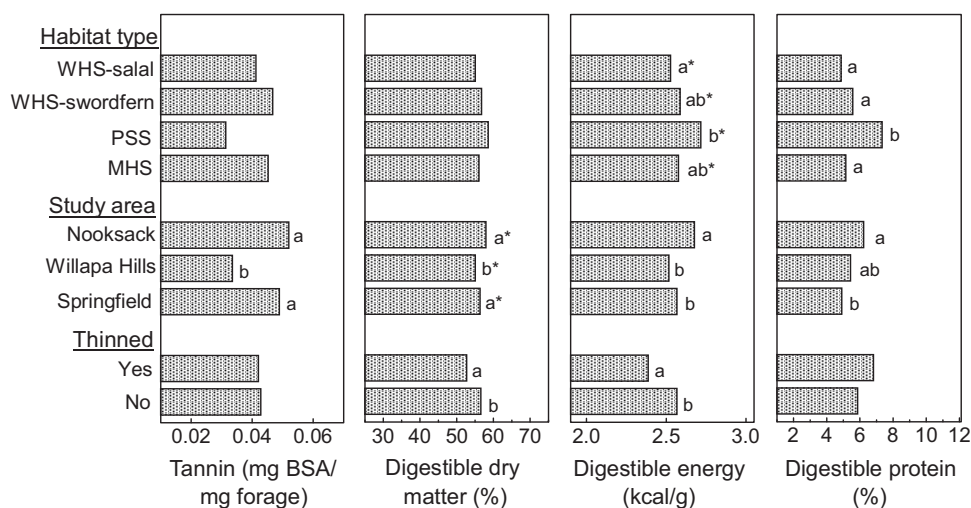


Figure 29. Nutritive value of elk diets among 4 habitat types, between thinned and unthinned stands, and among the Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within factors (e.g., habitat type), horizontal bars with different letters differ significantly ($P \leq 0.05$; when letters have asterisks, then $0.05 < P \leq 0.10$). Habitat codes are WHS = western hemlock series; PSS = Pacific fir series; MHS = mountain hemlock series; WHS-salal and WHS-swordfern = 2 plant association groups in the WHS (Table 7).

but perhaps was sufficiently abundant for calves to use effectively. When expressed as total kg per elk-day of use, NeuSpp and AccSpp exhibited the highest correlation of the forage variables with calf growth (Fig. 55), although neither was significantly correlated. Calves often exited the pens to feed, so they probably could reduce limitations in forage abundance apparently experienced by their mothers. Calf growth was unrelated to change in IFBF of their mothers ($P = 0.19$) and date ($P = 0.86$).

The best IFBF–nutrition model from stepwise regression included date ($P = 0.057$) and DE intake rate ($P = 0.003$; Table 10). The IFBF–forage biomass regression included date ($P = 0.044$) and a logarithmic transformation of AccSpp biomass per elk-use day ($P = 0.003$) and accounted for 66% of the variation

in change in IFBF (Table 10). No other independent variables were significant ($P > 0.18$). The calf growth–nutrition regression included dietary DE and DP intake rate as dependent variables (Table 10). Probability levels and partial r^2 for dietary DE and DP were nearly identical ($P = 0.011$ vs. 0.013), indicating approximately equal contributions of the 2 variables. The calf growth–forage biomass regression was not significant, however, and only the logarithm of AccSpp per elk use day was included in the model (i.e., the same model as that in Fig. 55; Table 10).

Nutrition Models

The initial analyses of dietary DE illustrated that influences of AccSpp, NeuSpp, and, to some extent, SelSpp were nonlinear,

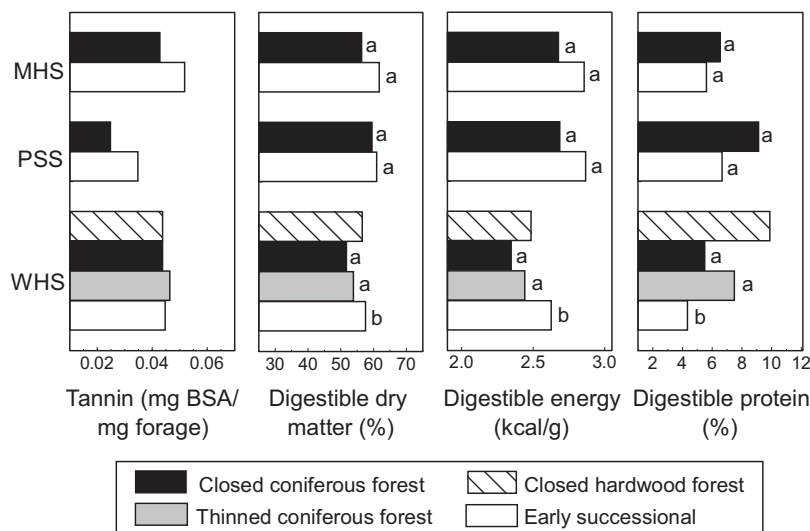


Figure 30. Nutritive value of elk diets between early seral stages and closed-canopy forests in the western hemlock (WHS), Pacific silver fir (PSS), and mountain hemlock (MHS) habitat types and between thinned and unthinned coniferous forests in the WHS type at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002 (Table 7). Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Data of hardwood forests ($n = 3$) are presented but were excluded from all analyses. Within habitat types, bars with different letters differ significantly ($P \leq 0.05$). Relevant comparisons in the WHS are between thinned versus early successional stands and between closed coniferous forests versus early successional stands; appropriate results for thinning effects (thinned forests vs. unthinned forests across the same range of stand age) are in Fig. 29.

Table 7. Initial analysis of covariance (ANCOVA) results for dietary quality variables of elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Covariates marked with an * or ** are significant at $0.05 < P \leq 0.10$ or $P \leq 0.05$, respectively.

Dependent variable ^a	<i>n</i>	<i>R</i> ²	<i>P</i>	Covariate of interest ^b	Covariates	Figure
Tannin	72	0.21	0.017	SA	SA**, HB _{WHS} , TH, DT, CC	29
Tannin	53	0.25	0.018	TH	SA**, HB _{WHS} , TH, DT	29
Tannin	86	0.21	0.019	HB _{All}	SA**, HB _{All} , TH, DT, CC	29
Tannin	86	0.20	0.01	SUCC	SA**, HB ₃ , SUCC, DT	30
Tannin	86	0.21	0.019	DT, CC	SA**, HB _{All} , TH, DT, CC	31, 33
Tannin	85	0.22	0.015	AGE	SA**, HB _{All} , TH, DT, AGE	32
Tannin	89	0.27	<0.001	FG	SA**, DT, (A**, N**, S)	34
Tannin	89	0.19	0.002	FG	SA**, DT, ALL	
DE	72	0.48	<0.001	SA	SA**, HB _{WHS} , TH, DT*, CC**	29
DE	53	0.28	0.006	TH	SA**, HB _{WHS} , TH**, DT	29
DE	86	0.57	<0.001	HB _{All}	SA**, HB _{All} , TH, DT*, CC**	29
DE	86	0.46	<0.001	SUCC	SA*, HB ₃ , SUCC*, DT	30
DE	86	0.57	<0.001	DT, CC	SA**, HB _{All} , TH, DT*, CC**	31, 33
DE	85	0.56	<0.001	AGE	SA**, HB _{All} , TH, DT, AGE**	32
DE	88	0.57	<0.001	FG	SA**, DT, (A, N*, S**, N × S**)	35
DE	88	0.38	<0.001	FG	SA**, DT, ALL**	
DP	72	0.53	<0.001	SA	SA**, HB _{WHS} , TH, DT**, CC**	29
DP	53	0.29	0.006	TH	SA**, HB _{WHS} , TH, DT**	29
DP	86	0.52	<0.001	HB _{All}	SA**, HB _{All} , TH, DT**, CC**	29
DP	86	0.46	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT**	30
DP	86	0.52	<0.001	DT, CC	SA**, HB _{All} , TH, DT**, CC**	31, 33
DP	85	0.51	<0.001	AGE	SA**, HB _{All} , TH, DT**, AGE**	32
DP	88	0.46	<0.001	FG	SA**, DT***, (A**, N**, A × N**, S)	39
DP	88	0.37	<0.001	FG	SA**, DT***, ALL**	39

^a Dependent variable codes are tannin = mg bovine serum albumin [BSA] precipitate/mg plant tissue; DE = digestible energy (kcal/g); DP = digestible protein (%).

^b Covariate of interest was covariate for which the analysis was conducted; additional covariates were included to control for their effects. Covariate codes are SA = study area; HB_{WHS} = habitat types in the western hemlock series (WHS-salal and WHS-swordfern); HB₃ = includes Pacific silver fir series (PSS), mountain hemlock series (MHS), and both WHS combined; HB_{All} = all 4 habitat types; TH = thinned (yes or no); DT = date (month number + [day/31.1]); SUCC = successional stage (early seral or closed-canopy forest); CC = overstory canopy cover (%); AGE = stand age (years); FG = forage groups (kg/ha) and includes A = avoided species, N = neutral species, S = selected species, and ALL = all species.

and consistent differences of DE existed between the high-elevation PSS and MHS habitats versus low-elevation WHS habitats. We developed equations for the 2 WHS habitat types separately. Although SelSpp generally failed to influence dietary DE strongly, we nevertheless included this variable in our analyses because of the strong affinity elk exhibited for these species; prediction models that include SelSpp may have greater management value than those that do not.

Beginning with the WHS and data from all study areas pooled, we used the asymptotic equation developed previously that included only AccSpp (Fig. 56) as a basis for comparing to more

complicated multiple regressions with SelSpp and NeuSpp. We compared 2 multiple regression formulations: 1) main effects of SelSpp and NeuSpp with their interaction term; and 2) SelSpp and NeuSpp but with AccSpp² instead of the 2-way SelSpp × NeuSpp interaction. The interaction of SelSpp and NeuSpp and the AccSpp² terms provided a basis for the equations to reflect the nonlinear nature of the basic forage abundance-DE relation. We selected the formulation that provided the highest adjusted *R*² and lowest *S_{y.x}*, added dummy variables representing study area to evaluate the need for separate equations for each study area, and added date as a check to confirm that this variable remained

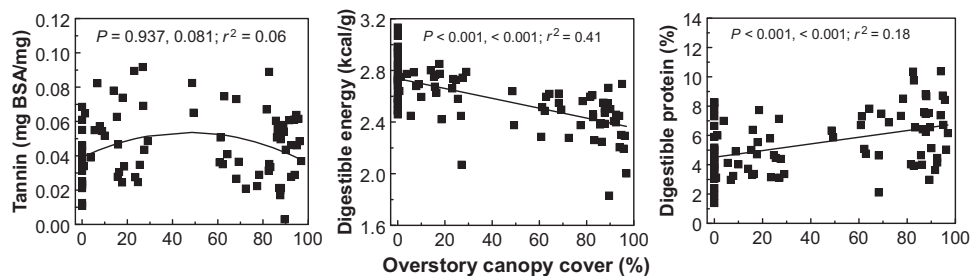


Figure 31. Tannin astringency, digestible energy, and digestible protein content of elk diets in relation to overstory canopy cover at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within each graph, the first *P* value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 7). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second *P* value and the *r*² are for the relation depicted in each graph. The first *P* value is relevant if the relation is linear; the second *P* value is of interest if the relation is nonlinear.

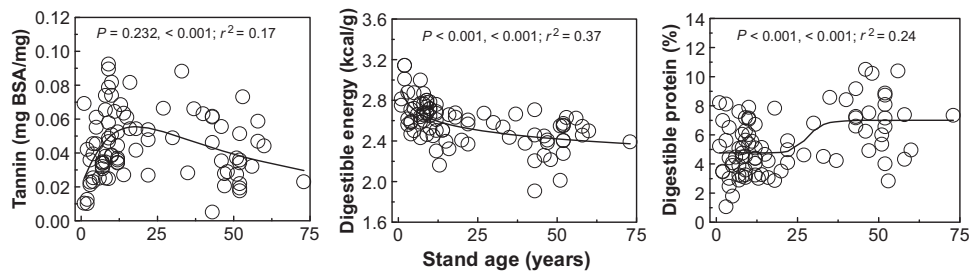


Figure 32. Tannin astringency, digestible energy, and digestible protein content of elk diets in relation to stand age at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and stand age (Table 7). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

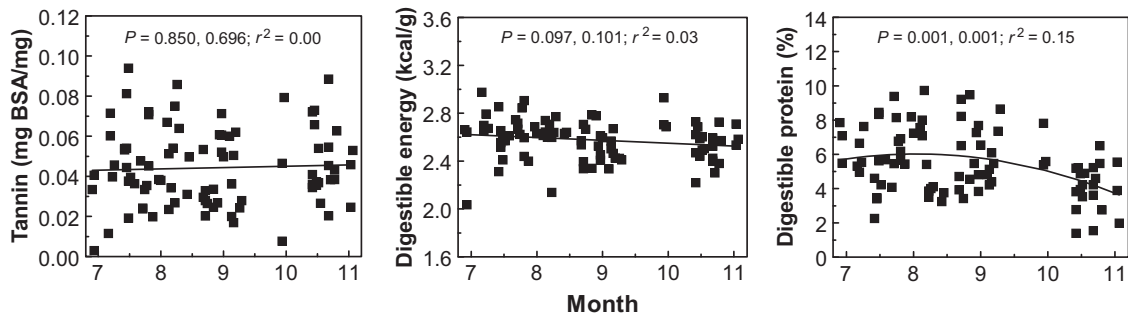


Figure 33. Tannin astringency, digestible energy, and digestible protein content of elk diets in relation to date at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 7). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

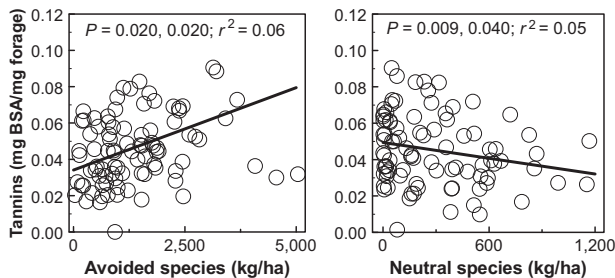


Figure 34. Relations of tannin astringency in elk diets with abundance of avoided and neutral plant species at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or total forage, study area, and date, 2 ANCOVAs per dependent variable (Table 7). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

an unimportant influence on dietary DE. All variables in both multiple regression models contributed significantly ($P < 0.003$), but the multiple regression with NeuSpp, SelSpp, and their interaction was marginally superior to the equation with NeuSpp, SelSpp, and AccSpp². The performance of the multiple regression equation was only slightly better than the exponential equation using only AccSpp in WHS habitats (Fig. 56A,B; Table 11). We present both as equally useful equations (Table 11). In the higher-elevation PSS and MHS habitats, we again found little difference in predictions of DE between the exponential model versus a multiple regression with NeuSpp, SelSpp, and their interaction (Fig. 56C; Table 11).

As we found before, date was uninfluential when added to the equation, but interactions existed between dummy variables for the study areas and NeuSpp ($P = 0.008$) and NeuSpp \times SelSpp ($P = 0.012$) that largely reflected a pattern of greater DE at Nooksack (Fig. 56B). Thus, we developed a multiple regression model for each study area (Table 11). Terms for NeuSpp and the NeuSpp \times SelSpp interaction were significant or approached significance in each of the 3 models ($P < 0.074$). The term for SelSpp was significant in the Willapa Hills and Springfield models ($P < 0.039$) although it was not in the Nooksack model

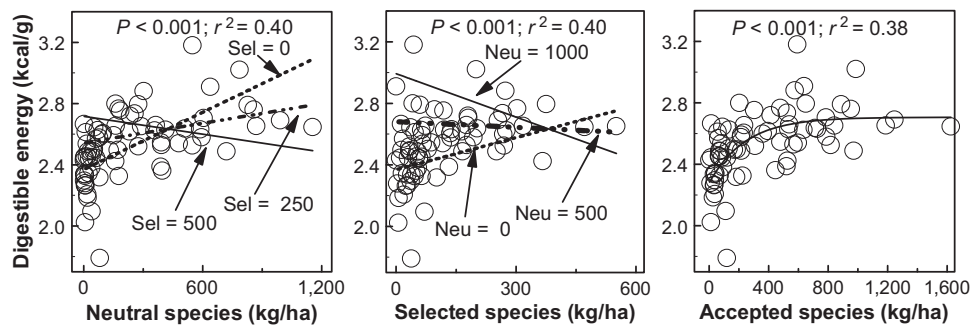


Figure 35. Relations of digestible energy (DE) in elk diets with abundance of neutral (neu), selected (sel), and accepted plant species at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Units for tannin astringency are mg of bovine serum albumin (BSA) precipitated/mg of plant tissue. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or total forage, study area, and date, 2 ANCOVAs per dependent variable (Table 7). For the neutral and selected species graphs, the 3 regression lines illustrate the neutral \times selected species interaction effect on DE content of elk diets. Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data.

($P=0.55$), but we retained all 3 terms in each of the 3 models (Table 11).

Development of regression equations for DE intake per minute included covariates that influenced forage intake rates and dietary DE levels and the nonlinear nature of both. Thus, we considered the main and interactive effects of AvdSpp and AccSpp, AccSpp^2 (providing a basis for nonlinear influences of this forage category), date, thinning, study area, and high- and low-elevation habitats (using dummy variable coding for the latter 3 covariates). We considered only AccSpp versus SelSpp and NeuSpp separately to simplify because predicting intake rate of DE was potentially more complicated, requiring a greater pool of predictor variables, than dietary DE. Because we found no significant effects of habitat type on any of our DE intake variables, we pooled all data across habitat types for our stepwise analysis but included the dummy variables for high- and low-elevation habitats as a check for significance of habitat type in our stepwise regressions.

The per-minute DE intake model included abundance of AccSpp ($P < 0.001$), AvdSpp ($P = 0.002$), AccSpp^2 ($P = 0.037$),

the interaction ($P = 0.011$) between AvdSpp and AccSpp, date ($P = 0.010$), thinning ($P = 0.072$), and study area (lower at Willapa Hills [$P = 0.032$] and Springfield [$P = 0.010$] than at Nooksack; Table 11). The pattern of a positive effect of AccSpp combined with a negative effect of AccSpp^2 corresponded to that found for dietary DE levels above. The pattern of a positive effect of AvdSpp combined with a negative effect of the AvdSpp \times AccSpp interaction corresponded to that found for forage dry matter intake described above.

Our findings described for DP analyses above indicated dietary DP and DP intake rate were little influenced by abundance of vegetation in our forage selection classes but were influenced by date, overstory canopy cover, habitat type, thinning, and soil moisture as indexed by our indicator plants of relative wet conditions. For stepwise regression, we therefore simplified the plant selection groups to AccSpp and AvdSpp and their log and quadratic transforms. We included interactions of these forage classes with overstory canopy cover, and included canopy cover plus logarithmic and quadratic versions, date, and the dummy variables for our high- and low-elevation habitats and study area. No interactions included these study-area dummy variables. We included 1 variable representing high soil moisture (sum of salmonberry, swordfern, red alder, and lady-fern abundance as proportion of AllSpp), and interactions of both with overstory canopy cover. The pool of covariates was the same for dietary DP and per-minute intake rate of DP.

Selected covariates for DP and intake of DP per minute regressions were similar (Table 12). The $\log \text{AccSpp} \times$ canopy cover interaction ($P < 0.001$), date ($P < 0.001$), wet site indicators ($0.001 \leq P \leq 0.013$), and high-versus low-elevation habitat types ($P \leq 0.067$) were included in both models. Study-area influences were significant only for dietary DP (higher at Nooksack), and thinning was significant only for DP intake rate (higher in thinned stands; $P = 0.017$). Overstory canopy cover, either as a main effect or as an interaction with our wet-site indicators ($0.002 \leq P \leq 0.083$), had a depressing effect on DP, suggesting that DP increased in stands with high AccSpp as long as canopy cover was moderate.

Using paired t -tests of observed and predicted levels of dietary DE and DP and intake rates by habitat type, successional stage, study area, and thinning treatments as a check for model errors,

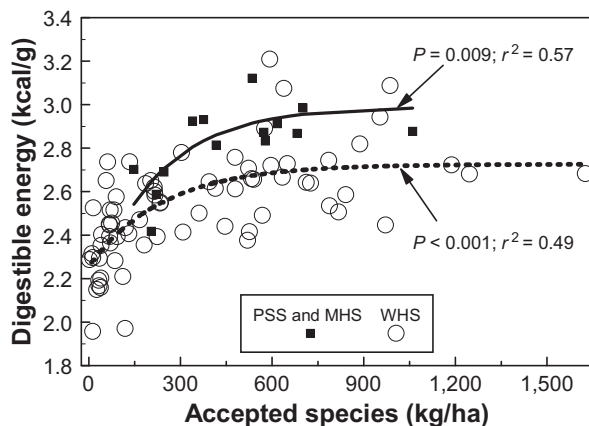


Figure 36. Exponential relationships between digestible energy (DE) in elk diets and abundance of accepted plant species for the high-elevation Pacific silver fir (PSS) and mountain hemlock (MHS) habitats combined and low-elevation western hemlock (WHS) habitats at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Data are in original units (not residuals).

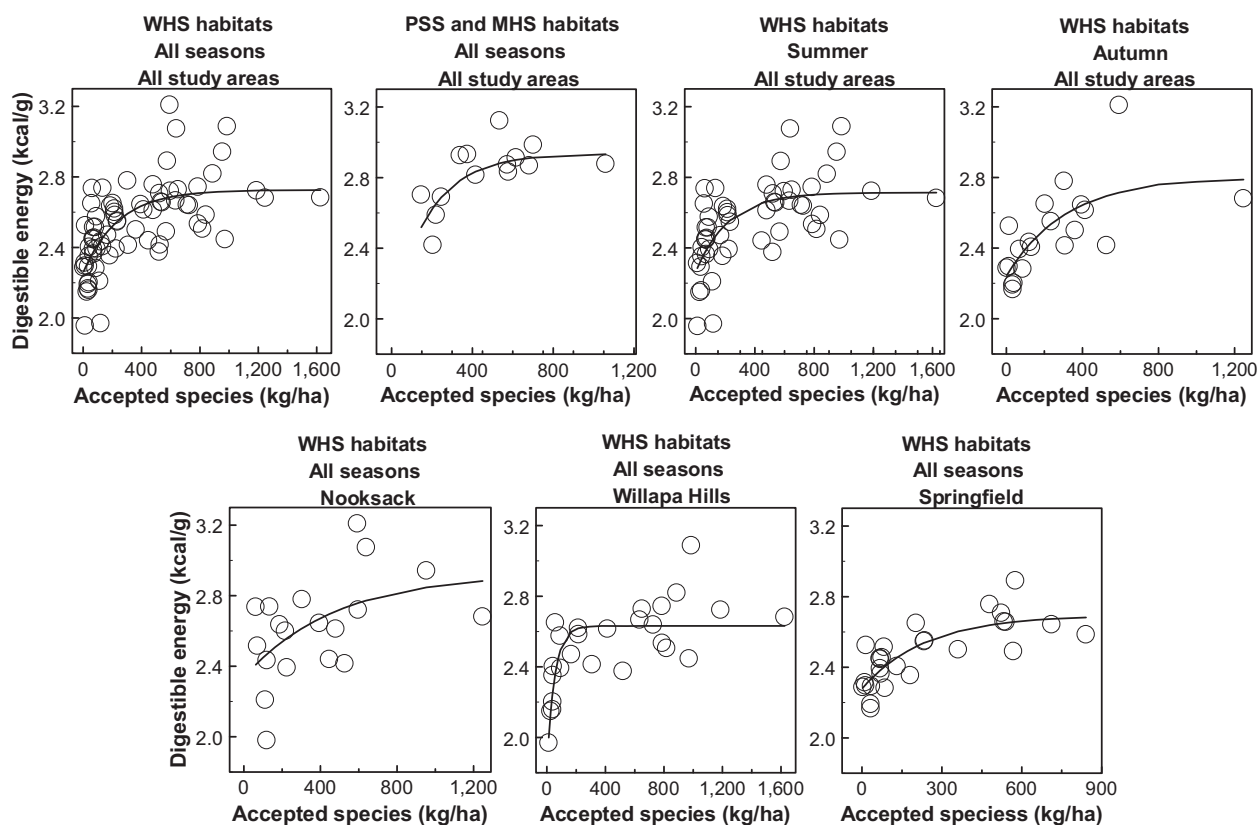


Figure 37. Exponential relations of digestible energy in elk diets and abundance of accepted plant species by habitat types, seasons, and study areas at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Habitat codes are WHS = western hemlock series; PSS = Pacific silver fir series; and MHS = mountain hemlock series. Data are in original units (not residuals), and relationships depicted in all graphs are significant ($P < 0.05$).

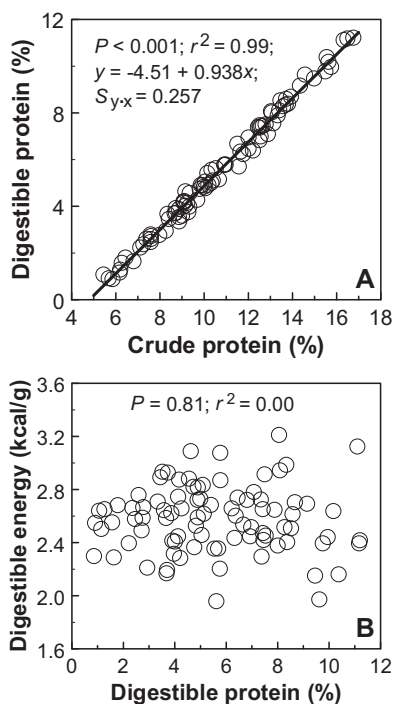


Figure 38. Relations between dietary crude protein and digestible protein (A) and dietary digestible energy and digestible protein (B) in elk diets at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. $S_{y \cdot x}$ = standard error of the estimate.

we found no significant differences ($P > 0.10$) for either of our DE variables (Fig. 57A,B). We found significantly higher predicted estimates of dietary DP and DP intake rate for high-elevation habitats in closed-canopy forests, although the magnitude of the differences was biologically negligible (Fig. 57C,D).

Illustrating successional trajectories of diet DE and DP variables using the predicted values of variables in combination with actually measured habitat variables available for the full macroplot data set ($n = 349$) offered several advantages versus DE and DP values actually measured in elk macroplots ($n = 89$). These advantages included a means of demonstrating patterns among study areas, habitat types, and other factors with a data set where most macroplots were randomly selected and thus more representative of actual habitat conditions on our study areas than elk macroplots. Doing so also provided a larger data set with greater replication in a variety of plant community types than represented by the elk macroplots.

Our projected trajectories illustrated a number of important patterns of ecological and management interest (Figs. 58–62). First, through 650 years of forest succession, our data indicated a remarkably short time of DE adequacy that was limited to early successional stages, where adequacy is defined as nutrition levels relative to those required for lactating female elk in summer and early autumn. These data (Figs. 58 and 59) illustrate important habitat \times time interactions, with higher DE levels persisting

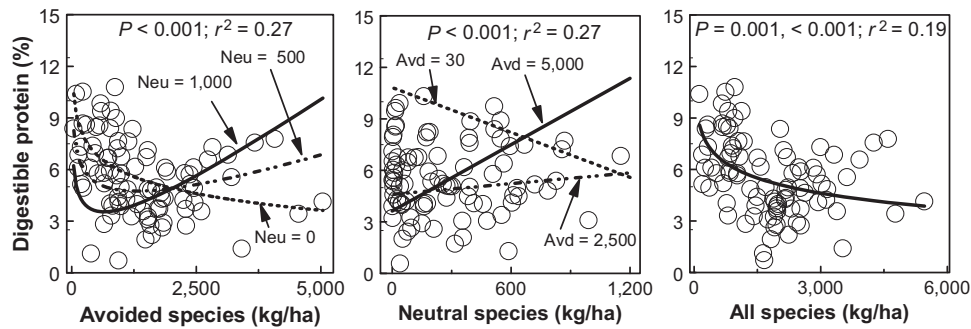


Figure 39. Relations between digestible protein in elk diets and abundance of avoided (avd), neutral (neu), and all plant species at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or total forage, study area, and date, 2 ANCOVAs per dependent variable (Table 7). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. For the avoided and neutral species graphs, the 3 regression lines illustrate the avoided \times neutral species interaction effect on dietary digestible protein. For the all species graph, the second P value and the r^2 are for the relation calculated via nonlinear regression. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

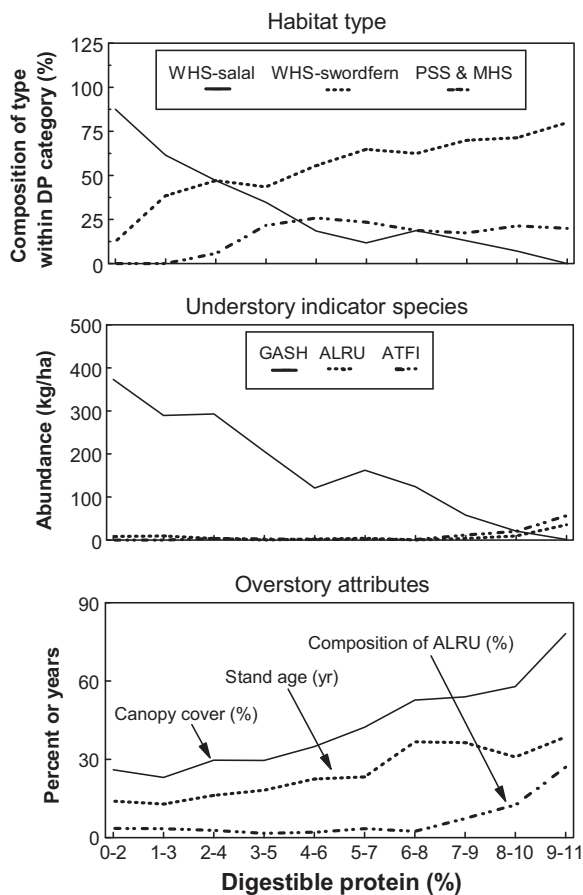


Figure 40. Relations between dietary digestible protein (DP) in elk diets and selected plant community attributes at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Data values are means of each attribute for each 3-percentage point category of DP. For each protein category, legend codes are WHS-salal = percent of macroplots in the western hemlock-salal habitat; WHS-swordfern = percent of macroplots in the western hemlock-swordfern habitat; PSS and MHS = percent of macroplots in the Pacific silver fir or mountain hemlock habitats; GASH (kg/ha) = abundance of salal (*Gaultheria shallon*); ALRU (kg/ha) = abundance of red alder (*Alnus rubra*); and ATFI (kg/ha) = abundance of ladyfern (*Athyrium filix-femina*). In the overstory attributes graph, we present mean canopy cover, stand age, and percent composition of red alder trees for each category of DP.

longer in PSS and MHS than in WHS. Second, relatively strong patterns evident for DE variables did not necessarily hold for DP variables. Levels of DP tended to show moderate increases from stands 2–3 years old to stands 20–40 years old, in contrast to DE levels in elk diets (Fig. 58 vs. Fig. 60), with little evidence of additional change thereafter. However, the trend of increasing dietary DP levels up to age 20–40 was not evident in DP intake per minute, indicating that the trend of lower dietary DP levels in stands <10 years was largely compensated by greater forage intake rates (Fig. 60 vs. Fig. 61). Third, the predictions indicate the greatest variation in DP variables, particularly DP intake, was due to differences among habitat types, whereas greatest variation in DE variables was due to variation in stand age (i.e., early seral vs. closed-canopy forests; Figs. 58–61). Fourth, once again in contrast to dietary DE and intake rate of DE, our data suggested that DP measures were not strongly inadequate or limiting except in WHS-salal habitats, no matter the successional stage (Figs. 60 and 61). Finally, predictions of DE and DP intake dynamics suggested moderate, positive influences of thinning in the WHS that varied among study areas, although our sample size of thinned stands was low (Fig. 62).

DISCUSSION

Our study supports the hypothesis that nutritional resources in the preponderance of habitat types in Pacific Northwest forests are inadequate to satisfy dietary DE requirements in summer and early autumn for lactating females and their offspring. In trials to evaluate body fat dynamics and calf growth as a function of vegetation characteristics available to them, elk lost body fat and calf growth was depressed in all trials conducted, markedly in some cases. Together, these findings provide strong support for the hypothesis that inadequate summer nutrition accounts for low pregnancy rates and autumn body fat levels previously reported for the region (Trainer 1971, Harper 1987, Stussy 1993, Cook et al. 2013).

Our findings clearly support the hypothesis that elk nutrition is strongly linked to seral stage and ecological site conditions and, consequently, also demonstrate that nutrition is a spatially and temporally predictable attribute across landscapes of the region. Our elk acquired dietary DE levels that often exceeded DE

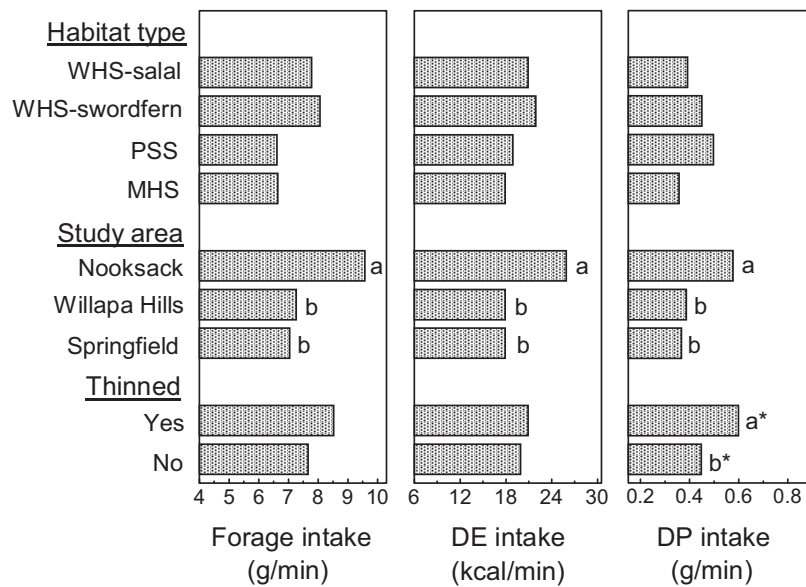


Figure 41. Forage, digestible energy (DE), and digestible protein (DP) intake rates of elk among 4 habitat types, between thinned and unthinned stands, and among Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within factors (e.g., habitat type), horizontal bars with different letters differ significantly ($P < 0.05$; when letters have asterisks, then $0.05 < P \leq 0.010$). Habitat codes are WHS = western hemlock series; PSS = Pacific fir series; MHS = mountain hemlock series; and WHS-salal and WHS-swordfern = 2 plant association groups in the WHS (Table 8).

requirement in early seral stages in the higher-elevation PSS and MHS types, usually at or above requirement in the WHS-swordfern type, and near requirement in the WHS-salal type. Once forest canopies closed, however, dietary DE and DE intake rate declined to levels below requirement, usually 2.3–2.6 kcal/g and 10,000–18,000 kcal/day (Figs. 58 and 59). These levels greatly reduce juvenile growth, pregnancy rates in lactating females, body fat in autumn, and may increase probability of overwinter mortality (Cook et al. 2004). As pronounced as the influences of forest succession and ecological conditions were on dietary DE and DE intake rates, such was not the case for DP. Instead, date, soil moisture, perhaps soil nitrogen levels, and, to some extent, habitat type influenced dietary DP and intake rates of DP.

The transition from early seral communities to closed-canopy forests marked a clear threshold between nutritionally adequate environments to nutritionally inadequate environments. Thus, the mix of seral stages and ecological site potentials may greatly affect the overall adequacy of nutritional resources on Pacific Northwest landscapes. In light of the strong linkages between elk nutrition, forest succession, and ecological site potentials, our study indicates that forest management can play a strong, positive role in modifying nutritional environments for elk. Because dietary DP was inconsistently affected by disturbance regime and subsequent succession, and because DP was less limiting than DE (see also Alldredge et al. 2002, Cook 2002, Beck and Peek 2005), evaluating and managing nutritional resources in light of DE will likely be of greater value than for DP. McArt et al. (2009) argued that DP was superior to DE as a measure of nutritional value in moose, but the strong influences of DE on over-summer body fat accretion and juvenile growth are well documented in deer and elk (Verme and Ozoga 1980; Cook et al. 1996, 2004), and DE is often reported to be a more useful measure than protein at least in

some ecological settings (Verme and Ozoga 1980, Skogland 1991, Illius and Gordon 1999, Searle et al. 2007).

Our findings also demonstrated that foraging behavior of elk varied with species composition and abundance of vegetation, evidently to compensate for limited foraging options available to them in many plant communities. Our elk exhibited strong and consistent selection for many plant species to acquire diets relatively high in DE, and increasingly consumed forage of relatively low palatability only when abundance of palatable species was low. This switch helped offset declines in DE intake rate, although dietary DE levels declined. By increasing their rate of travel while foraging, elk compensated for plant communities with very low abundance of forage. Also, increasing bite rate helped to compensate as bite mass declined, time spent feeding at night increased modestly in macroplots that provided low abundance of total forage or relatively low dietary DE levels, and rumination time increased particularly in response to high dietary fiber levels (NDF) of consumed forage. These behavioral and physiological strategies helped elk mitigate for declining abundance of relatively high-quality forage such that nutritional outcomes were robust to substantial variation in overall forage quality and quantity. Nevertheless, these strategies were insufficient to compensate fully for very low abundance of high-quality forage typically present under closed forest canopies.

Mechanisms Linking Plant Communities and Foraging Responses

Forest management and succession.—The wet and relatively warm climate of the temperate rainforests of our study area supported high vegetative productivity, among the highest on earth (Franklin and Dyrness 1988), and supported rapid rates of plant succession following disturbance, particularly at low and moderate elevations of the study area. Foresters applied

Table 8. Initial analysis of covariance (ANCOVA) results for intake rate variables of elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Covariates marked with an * or ** are significant at $0.05 < P \leq 0.10$ or $P \leq 0.05$, respectively.

Dependent variable ^a	<i>n</i>	<i>R</i> ²	<i>P</i>	Covariate of interest ^b	Covariates	Figure
DM/min	72	0.36	<0.001	SA	SA**, HB _{WHS} , TH*, DT**, CC**	41
DM/min	53	0.22	0.032	TH	SA*, HB _{WHS} , TH, DT	41
DM/min	86	0.33	<0.001	HB _{All}	SA**, HB _{All} , TH*, DT**, CC**	41
DM/min	86	0.34	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT*	42
DM/min	86	0.33	<0.001	DT, CC	SA**, HB _{All} , TH*, DT**, CC**	43, 45
DM/min	85	0.32	<0.001	AGE	SA**, HB _{All} , TH*, DT**, AGE**	44
DM/min	89	0.36	<0.001	FG	SA**, DT**, (A*, N*, A × N**, S)	46
DM/min	89	0.26	<0.001	FG	SA**, DT**, ALL	46
DM/24-hr	27	0.44	0.025	SA	SA*, HB _{WHS} **, TH, DT, CC	
DM/24-hr	24	0.25	0.122	TH	SA, TH*, DT	
DM/24-hr	34	0.38	0.060	HB _{All}	SA, HB _{All} , TH, DT, CC	
DM/24-hr	33	0.28	0.155	SUCC	SA**, HB ₃ , SUCC, DT	
DM/24-hr	34	0.38	0.060	DT, CC	SA, HB _{All} , TH, DT, CC	
DM/24-hr	33	0.39	0.050	AGE	SA, HB _{All} , TH*, DT, AGE	
DM/24-hr	35	0.32	0.076	FG	SA**, DT, (A**, N, A × N**, S)	48
DM/24-hr	35	0.14	0.188	FG	SA**, DT, ALL	
DE/min	72	0.42	<0.001	SA	SA**, HB _{WHS} , TH, DT**, CC**	41
DE/min	53	0.24	0.021	TH	SA**, HB _{WHS} , TH, DT	41
DE/min	86	0.41	<0.001	HB _{All}	SA**, HB _{All} , TH, DT**, CC**	41
DE/min	86	0.40	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT**	42
DE/min	86	0.41	<0.001	DT, CC	SA**, HB _{All} , TH, DT**, CC**	43, 45
DE/min	85	0.39	<0.001	AGE	SA**, HB _{All} , TH, DT**, AGE**	44
DE/min	89	0.45	<0.001	FG: A, N, S	SA**, DT, A, N**, A × N**, S*, N × S**	
DE/min	89	0.45	<0.001	FG: ALL	SA**, DT**, ALL**, A × H**, A × N**, S**, N × S**	
DE/24-hr	27	0.41	0.038	SA	SA*, HB _{WHS} , TH, DT, CC	
DE/24-hr	24	0.20	0.210	TH	SA, TH, DT	
DE/24-hr	34	0.36	0.083	HB _{All}	SA*, HB _{All} , TH*, DT, CC	
DE/24-hr	33	0.30	0.116	SUCC	SA**, HB ₃ , SUCC, DT	
DE/24-hr	34	0.36	0.083	DT, CC	SA*, HB _{All} , TH*, DT, CC	
DE/24-hr	33	0.38	0.059	AGE	SA, HB _{All} , TH*, DT, AGE	
DE/24-hr	35	0.31	0.084	FG	SA**, DT, (A*, N, A × N*, S)	49
DE/24-hr	35	0.20	0.074	FG	SA**, DT, ALL	
DP/min	72	0.54	<0.001	SA	SA**, HB _{WHS} , TH**, DT**, CC	41
DP/min	53	0.46	<0.001	TH	SA**, HB _{WHS} , TH*, DT**	41
DP/min	86	0.52	<0.001	HB _{All}	SA**, HB _{All} , TH*, DT**, CC*	41
DP/min	86	0.51	<0.001	SUCC	SA**, HB ₃ , SUCC**, DT**	42
DP/min	86	0.52	<0.001	DT, CC	SA**, HB _{All} , TH*, DT**, CC*	43, 45
DP/min	85	0.50	<0.001	AGE	SA**, HB _{All} , TH*, DT**, AGE	44
DP/min	89	0.46	<0.001	FG	SA**, DT**, (A, N**, S)	
DP/min	89	0.40	<0.001	FG	SA**, DT**, ALL	
DP/24-hr	27	0.51	0.007	SA	SA**, HB _{WHS} , TH, DT, CC	
DP/24-hr	24	0.39	0.018	TH	SA*, TH**, DT	
DP/24-hr	34	0.52	0.004	HB _{All}	SA**, HB _{All} , TH, DT, CC*	
DP/24-hr	33	0.42	0.019	SUCC	SA, HB ₃ , SUCC**, DT	
DP/24-hr	34	0.52	0.004	DT, CC	SA**, HB _{All} , TH, DT, CC*	
DP/24-hr	33	0.57	0.003	AGE	SA**, HB _{All} , TH, DT, AGE	
DP/24-hr	35	0.43	0.004	FG	SA**, DT, (A*, N**, S)	50
DP/24-hr	35	0.33	0.006	FG	SA**, DT, ALL**	50

^a Dependent variable codes are DM = dry matter (g); DE = digestible energy (kcal); DP = digestible protein (%) each expressed as per minute during daylight hours (/min) or per 24-hour period (/24-hr).

^b Covariate of interest was covariate for which the analysis was conducted; additional covariates were included to control for their effects. Covariate codes are SA = study area; HB_{WHS} = habitat types in the western hemlock series (WHS-salal and WHS-swordfern); HB₃ = includes Pacific silver fir series (PSS), mountain hemlock series (MHS), and both WHS combined; HB_{All} = all 4 habitat types; TH = thinned (yes or no); DT = date (month number + [day/31.1]); SUCC = successional stage (early seral or closed-canopy forest); CC = overstory canopy cover (%); AGE = stand age (years); FG = forage groups (kg/ha) and include A = avoided species, N = neutral species, S = selected species, and ALL = all species.

even-aged regeneration tree harvests, often used herbicides to reduce residual understory vegetation soon after logging, planted conifer seedlings, and often used a release herbicide treatment to enhance growth of young conifer seedlings.

Rates of overstory and understory succession varied among ecological site potentials indexed by our habitat classification and, to a lesser extent, among the ecological provinces represented by our 3 study areas. Abundance of AccSpp in the WHS peaked at

300–800 kg/ha for 10–15 years after logging, but thereafter averaged <50 kg/ha and ≤10% of total understory vegetation. In the PSS and MHS, AccSpp peaked during 20 to 40 years after logging, but otherwise was ≤100 kg/ha and composed 10% to 30% of understory vegetation. In general, rates of overstory and understory succession were modestly faster in the WHS at Willapa Hills than Nooksack or Springfield probably because of wetter and warmer climate (Franklin and Dyrness 1988).

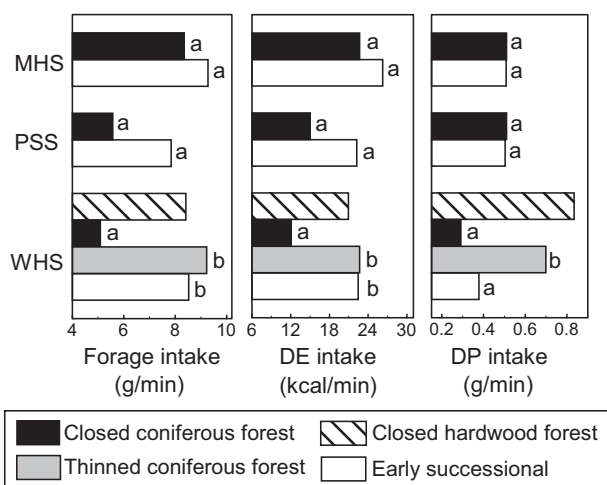


Figure 42. Forage, digestible energy (DE), and digestible protein (DP) intake rates of elk between early seral stages and closed-canopy forests in the western hemlock (WHS), Pacific silver fir (PSS), and mountain hemlock (MHS) habitat types and between thinned and unthinned coniferous forests in the WHS type at Nooksack, Willapa Hills, and Springfield study areas, 2000–2002. Data of hardwood forests ($n=3$) are presented but were excluded from all analyses. Within habitat types, bars with different letters differ significantly ($P < 0.05$, Table 8). Relevant comparisons in the WHS are between thinned versus early successional stands and between closed coniferous forests versus early successional stands; appropriate results for thinning effects (thinned forests vs. unthinned forests across the same range of stand age) are in Fig. 41.

Community-wide forage DE levels approached elk summer requirements only in early seral stages but were higher and persisted longer in succession in the PSS and MHS than in the WHS (Fig. 11). Higher forage DE levels in the PSS and MHS were probably due to 2 influences: 1) delayed phenology in the higher-elevation PSS and MHS (spring growth initiation after early Jun in the PSS and MHS vs. early Apr in the WHS) such that cell solubles were higher and fiber content was lower during much of summer (Hebblewhite et al. 2008); and 2) moderately lower dominance in the PSS and MHS of the plant groups with the lowest levels of DE (evergreen shrubs and ferns).

We were unable to evaluate herbicide effects because most of the stands we sampled, at least in the WHS and PSS, had been treated with herbicides. Use of herbicides to support growth of young conifers influences understory succession and was

perceived to be detrimental to elk and deer herds in the region (Washington Department of Fish and Wildlife 2006, Oregon Department of Fish and Wildlife 2008). Concerns were that use of herbicides greatly reduces the abundance of desirable early seral vegetation and increases the rate of conifer development and overstory closure. Nevertheless, nutritional value of early seral stages, despite herbicide treatments, exceeded that of any other forest successional stage. Using forage evaluation methods similar to ours in southwestern Washington, Geary (2014) reported that herbicides 1) reduced unpalatable legacy species such as swordfern and evergreen shrubs across most of the early seral period, 2) reduced palatable species for 2 years after the final herbicide treatment, 3) had little effect on abundance of palatable forage thereafter, and 4) had little effect on timing of the decline of forage in early seral communities as forest canopies closed. Those findings were largely consistent with ours except that we documented modestly greater abundance of palatable species (500–800 kg/ha; Fig. 14) the first 1–3 years after the final herbicide treatment than did Geary (2014; 400 kg/ha 1–2 years after herbicide application). Many of Geary's (2014) sampling sites were research plots initially designed for different studies, where applications of herbicides may have been better controlled and thus more effective than the operational treatments of our study. In addition, herbicide treatments applied in the early to mid-2000s that were evaluated by Geary (2014) may have been more effective at controlling competing vegetation than those used in the mid- and late 1990s, the period relevant to our study. Regardless, both studies indicated that abundance of palatable forage was much greater in early seral stands even during the first 2 years after herbicide application than in mid or late seral closed-canopy forests. Studies in other regions of North America documented highly variable influences of herbicide treatments ranging from short-term detriment to beneficial effects, depending on a host of site and treatment factors (Lautenschlager and Sullivan 2002).

The second silvicultural technique common in our area, commercial thinning, may increase production and diversity of understory vegetation by disturbing soils and understory vegetation, by increasing transmission of light to the forest floor, and by reducing competition between understory and overstory vegetation (Thomas et al. 1999). However, vegetation

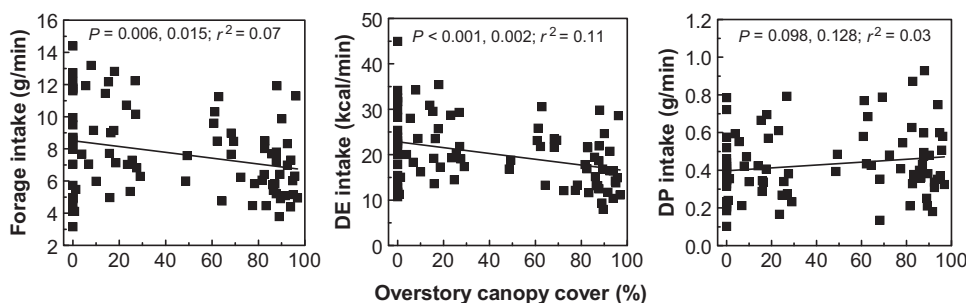


Figure 43. Forage, digestible energy (DE), and digestible protein (DP) intake rate of elk in relation to overstory canopy cover at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph calculated via linear or nonlinear regression techniques. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

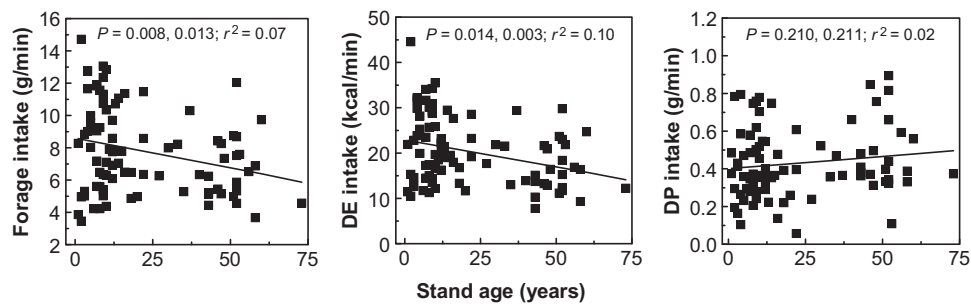


Figure 44. Forage, digestible energy (DE), and digestible protein (DP) intake rate of elk in relation to stand age at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph calculated via linear or nonlinear regression techniques. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

responses to thinning are variable, difficult to predict (Alaback and Herman 1988, Thomas et al. 1999), and may provide little improvement in forage for elk (Jenkins and Starkey 1996). We found relatively strong increases (usually $2\times$ greater) in abundance of total understory vegetation, despite only modest reductions in overstory canopy cover ($>65\%$ canopy cover in all thinned stands). However, the increases in abundance included both palatable and unpalatable vegetation (Table 3); abundance of AccSpp usually ranged ≤ 200 kg/ha (Appendix G); and community-wide forage DE levels were similar between thinned and unthinned stands. Therefore, the potential nutritional benefits to elk of thinning at least in the WHS evidently were substantially less than those from clearcut logging (Jenkins and Starkey 1996). Our thinning data from high elevation forests, however, was very limited, and findings for the WHS may not apply for the PSS and MHS.

Foraging behavior.—Our study illustrated a fundamental challenge facing large herbivores: abundance of low-quality vegetation is usually high and so it can be eaten rapidly, but daily intake is restricted by digestive limitations, whereas abundance of high-quality forage is usually low, and so it often cannot be eaten rapidly (Illius 1997). Herbivores may have 2 overall strategies to cope with this challenge: 1) seek diets consisting of relatively high-quality forage even if DE and nutrient intake rates are sacrificed to do so (dietary DE maximizing); and 2) seek diets

that maximize intake rates of DE and various nutrients even if dietary quality is sacrificed to do so (DE intake maximizing). If the former is the dominant strategy, then abundant low-quality food cannot appreciably substitute for low levels of high-quality food. If the latter dominates, then low-quality food may substitute for high-quality food if low-quality food is both abundant and offers high bite mass. We think that understanding which of these strategies elk use, and why, has important implications for advancing understanding of nutritional ecology and for developing effective habitat management strategies.

Elk employed several tactics to compensate for poor forage quantity and quality, some of which were relatively strong while others were weak. Increasing travel rates, bite rates, rumination time (albeit only measured during daylight hours), and total time spent foraging per 24 hours all were statistically significant tactics in response to inadequate nutritional resources. However, low coefficients of determination associated with these tactics suggest that elk used a variety of tactics simultaneously to compensate for inadequate nutritional resources, such that explanatory power of any single tactic was low.

Our elk foraged 11.5 hours in summer and 10.5 hours in autumn per 24-hour period on average. Thus, elk ostensibly could greatly increase daily DE intake by spending more hours feeding each day and should do so because daily DE intake averaged substantially below requirements, even in habitat types

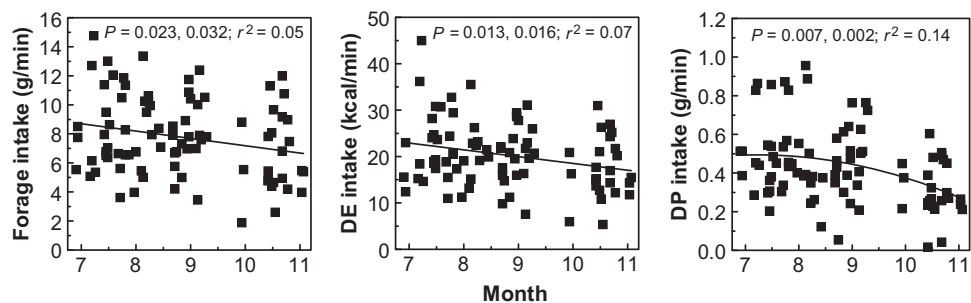


Figure 45. Forage, digestible energy (DE), and digestible protein (DP) intake rate of elk in relation to date at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included study area, habitat type, thinning, date, and canopy cover (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph calculated via linear or nonlinear regression techniques. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

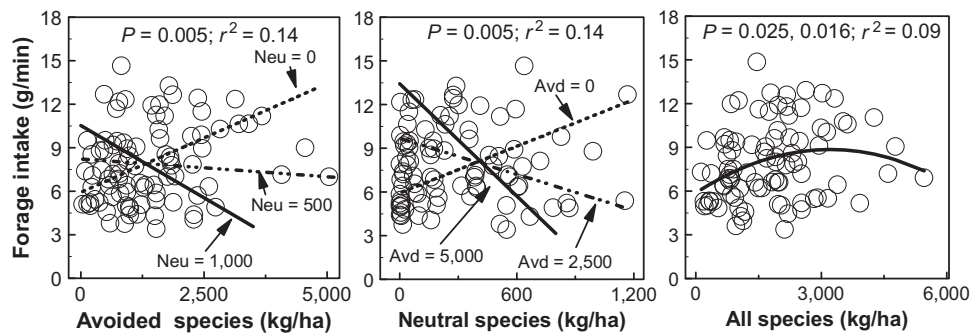


Figure 46. Relations between forage intake rate of elk and abundance of avoided (avd), neutral (neu), and all plant species at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or total forage, study area, and date, 2 ANCOVAs per dependent variable (Table 8). Data presented in graphs are residuals from the ANCOVAs added to the overall mean of the dependent variable to rescale residuals to the range of the original data. For the avoided and neutral species graphs, the 3 regression lines illustrate the avoided \times neutral species interaction effect on forage intake rate. For the all species graph, the second P value and the r^2 are for the relation depicted calculated via nonlinear regression; the first P value is relevant if the relation is linear, and the second P value is of interest if the relation is nonlinear.

where dietary DE satisfied requirements (Fig. 51). Instead of switching to lower-quality forage as abundance of AccSpp declined, why did our elk fail to increase the amount of time each day for locating and consuming those forages that best satisfied their needs? Moreover, many of those foraging tactics, including 24-hour foraging time, that elk potentially might use to

compensate for poor nutritional resources, evidently were reduced in autumn. Why would foraging effort decline in autumn just prior to winter, when starvation threatens?

Varying daily feeding time insufficiently to attain daily DE requirements was reported by others (Alden and Whittaker 1970, Chacon and Stobbs 1976), and the amount of time our elk foraged each day is similar to estimates reported elsewhere (Trudell and White 1981, Hudson and Nietfeld 1985, Watkins et al. 1991). Hudson and Nietfeld (1985) identified an upper limit of daily foraging time of 13 hours for elk. Explanations for this limit include fatigue of the jaw muscles (Penning et al. 1991, Illius 1997) and needs for rest, rumination, parental care, vigilance, and other such activities. Rumination is an obligate physiological process that increases as fiber intake increases; our elk spent on average about 4 hours of daylight in summer ruminating, and probably spent ≥ 2 hours ruminating at night, leaving ≤ 6 hours per 24 hours for all non-feeding, non-ruminating activities. Assuming that elk need to rest at least 3–5 hours a day, it seems clear why daily feeding time usually was less than 13 hours per day.

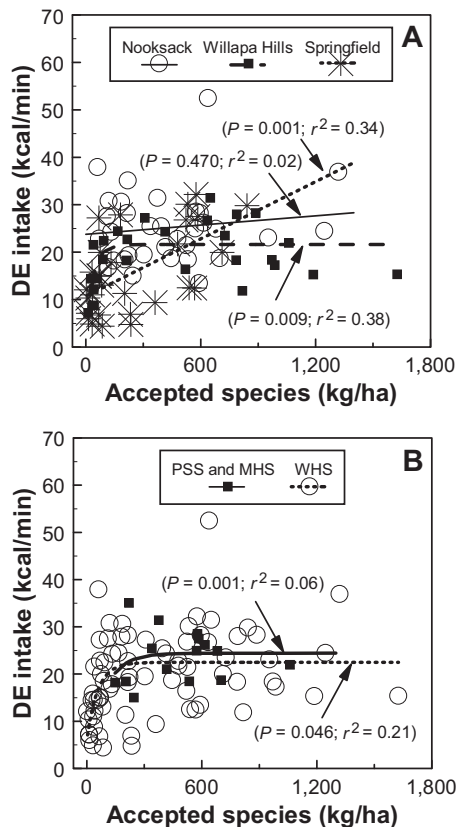


Figure 47. Relations between digestible energy (DE) intake rate of elk and abundance of accepted plant species by study area (A) and high- (Pacific silver fir [PSS] and mountain hemlock series [MHS]) and low-elevation (western hemlock series [WHS]) habitat types (B) at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Data are in original units.

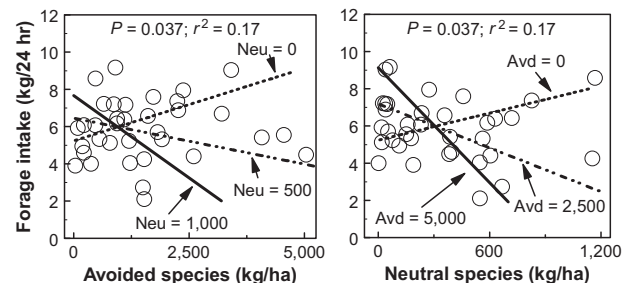


Figure 48. Relations between forage intake rate per 24 hours for elk and abundance of 2 forage categories at Nooksack and Willapa Hills study areas in western Oregon and Washington, 2001–2002. Within each graph, the P value is from the overall analysis of covariance (ANCOVA) that included abundance of selected, neutral (neu), and avoided (avd) plant species, study area, and date, 2 ANCOVAs per dependent variable (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The 3 regression lines in each graph illustrate the interaction between avoided and neutral species.

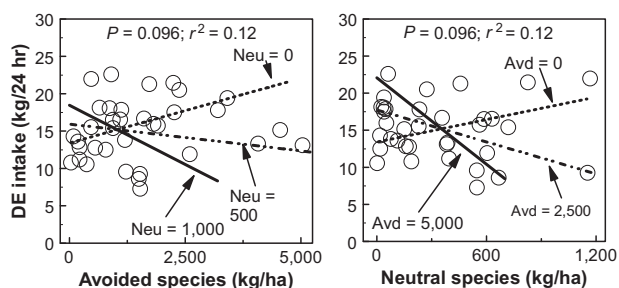


Figure 49. Relations of digestible energy (DE) intake rate per 24 hours of elk and abundance of 2 forage categories (avoided species [avd] and neutral species [neu]) at Nooksack and Willapa Hills study areas in western Oregon and Washington, 2001–2002. Within each graph, the P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or total forage, study area, and date, 2 ANCOVAs per dependent variable (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The 3 regression lines in each graph illustrate the interaction between avoided and neutral species.

Declining metabolic energy demands and a concomitant declining ability to consume and digest large amounts of food in autumn, in response to declining daylength, probably explain our observations of reduced foraging effort after summer. Not only did time spent foraging decline in autumn, so too did bite rate and forage, DE, and DP intake rates, although nutritional condition of the elk was lower in early autumn than in early summer. The apparent declines in foraging intensity may be related to changes in forage conditions, such as lower forage quality (Hudson and Haigh 2002). However, Cook et al. (2004) reported declines in daily intake of food beginning after mid-September in controlled studies of elk in 3 dietary quality treatment groups, ranging from strongly below to strongly above requirements. Because the declines were similar between very thin elk (body fat = 3–4%) and relatively fat elk (body fat = 17–18%; Cook et al. 2004: 34) fed constant quality, *ad libitum* hay and pellet diets, they concluded that the cause was likely a physiological response to declining daylength. Influences of declining photoperiod on hormones that reduce forage intake and metabolic rate in autumn is reasonably well documented (Arnold 1985, Hudson and Christopherson 1985). Declining metabolic rates may increase tolerance of nutritional deprivation

Table 9. Standardized regression coefficients of independent variables on intake rate per minute (min) and 24 hours (24-hr) of dry matter, digestible energy, and digestible protein for elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. All foraging variables were significant ($P \leq 0.048$) except where indicated (ns). These results were generated from 6 regression analyses, and for each, $P < 0.001$.

Independent variable	Dry matter (g)		Digestible energy (kcal)		Digestible protein (g)	
	Min	24-hr	Min	24-hr	Min	24-hr
Bite mass (g/bite)	0.88	1.11	0.869	1.109	0.546	0.674
Bite rate (bites/min)	0.62	0.75	0.522	0.734	0.322	0.444
Concentration ^a	na	na	0.245	0.186	0.743	0.927
Feeding (min/24 hr)	na	0.23	na	0.221	na	ns

^a Concentration of either digestible energy (kcal/g) or digestible protein (%) in elk diets.

and harsh weather in winter in northern ecosystems, although this contention remains debated (Silver et al. 1969 vs. Mautz et al. 1992). Further, metabolizable energy requirements of young-adult nonlactating female elk were estimated to be 64% higher in summer than in winter (Jiang and Hudson 1992), and declines in growth of juveniles in autumn and winter despite high-quality food are well documented for Cervidae (Verme and Ozoga 1980, Sibbald et al. 1993, Cook et al. 1996).

Our elk exhibited a relatively high degree of selection and avoidance for many plant taxa, which was evident even in stands that provided little AccSpp, and this evidently was a more consistent strategy to compensate for inadequate nutritional resources than travel and bite rates, foraging time, and rumination time. Accepted species consistently declined below 80% of diets only when their abundance was below about 200 kg/ha in the WHS, and failed to decline consistently at any abundance level of AccSpp that we recorded in the PSS and MHS (Fig. 63).

Our food habits results are generally consistent with findings reported for wild elk on landscapes with a mix of early and advanced seral stages. In our study, deciduous shrubs were a prominent component of AccSpp and typically dominated elk diets particularly in autumn when many forb taxa were senescent, although fool's huckleberry (*Menziesia ferruginea*) in high-elevation habitats and trailing blackberry at all elevations were notable exceptions. Forbs composed the second most common

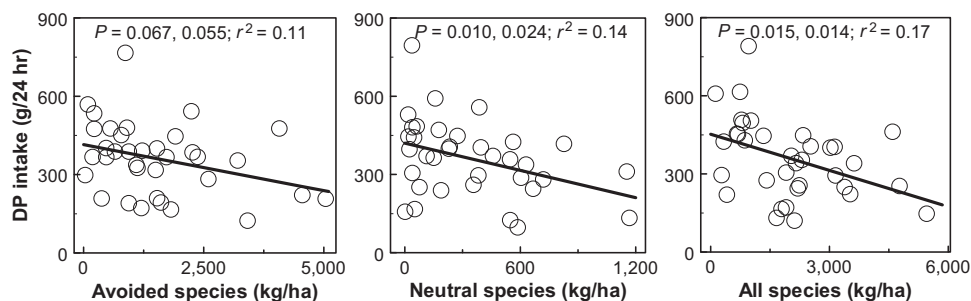


Figure 50. Relations of digestible protein (DP) intake rate per 24 hours of elk and abundance of 3 forage categories at Nooksack and Willapa Hills study areas in western Oregon and Washington, 2001–2002. Within each graph, the first P value is from the overall analysis of covariance (ANCOVA) that included the 3 forage groups or all species, study area, and date, 2 ANCOVAs for each dependent variable (Table 8). Data presented in graphs are residuals from the ANCOVAs, added to the overall mean of the dependent variable to rescale residuals to the range of the original data. The second P value and the r^2 are for the relation depicted in each graph. The first P value is relevant if the relation is linear; the second P value is of interest if the relation is nonlinear.

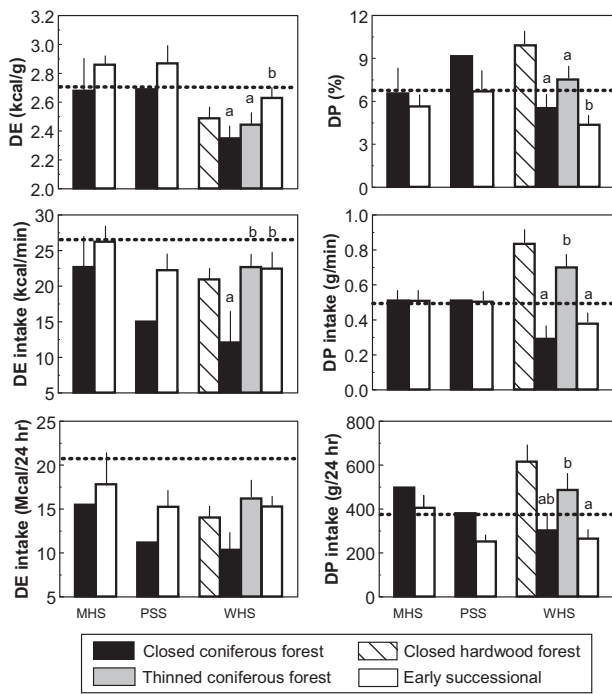


Figure 51. Summary of digestible energy (DE) and digestible protein (DP) intake dynamics of elk between early seral and closed-canopy forest by habitat type and thinned versus unthinned mid seral forests in the western hemlock series with estimates of requirements (horizontal, dotted line) included for lactating female elk in summer in western Oregon and Washington, 2000–2002. Data are pooled by Nooksack, Willapa Hills, and Springfield study areas for dietary DE and DP intake rate/minute, and are presented for Nooksack and Willapa Hills for DE and DP intake rate per 24 hours (we did not collect 24-hr data at Springfield). Habitat type codes are MHS = mountain hemlock series; PSS = Pacific silver fir series; and WHS = western hemlock series. Vertical bars are ± 1 standard error.

plant group in elk diets. Although we found little evidence of selection for forbs overall, several were among the most selected of all species, including queen's cup beadlely, Solomon plume (*Smilacina* spp.), Oregon oxalis, beadruby, and clover (*Trifolium*

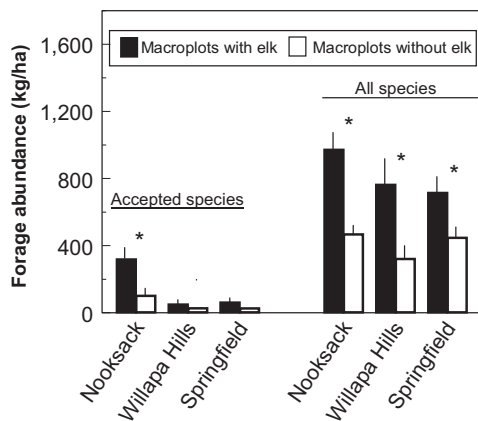


Figure 52. Abundance of accepted forage and total forage present in macroplots with elk and in macroplots without elk at 3 study areas in western Oregon and Washington, 2000–2002. Data are presented for macroplots located in closed-canopy forests, and indicate that stands selected for sampling with elk generally contained more forage than those without. Asterisks indicate statistically significant ($P < 0.05$) differences between elk-present and elk-absent bars within study areas. Vertical bars are ± 1 standard error.

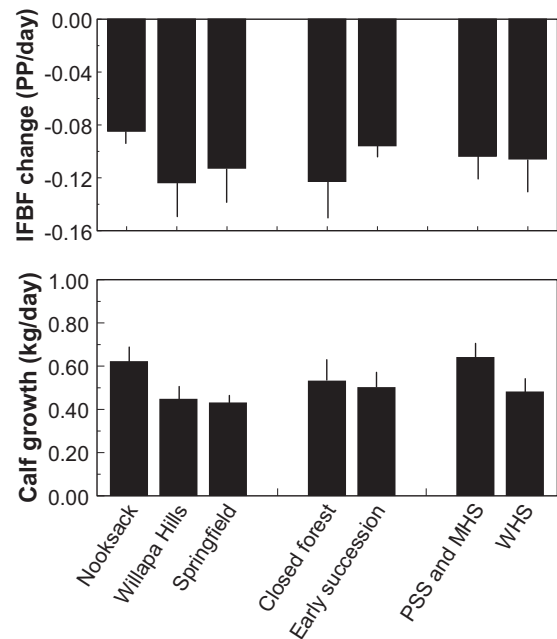


Figure 53. Change in ingesta-free body fat (IFBF), in percentage points (PP) per day, of adult lactating elk (A) and calf growth (B) by study area, forest seral stage, and habitat type at 3 study areas in western Oregon and Washington, 2000–2002. Habitat type codes are WHS = western hemlock series; PSS = Pacific silver fir; MHS = mountain hemlock series. Vertical lines represent ± 1 standard error.

spp.). Dietary composition of graminoids was secondary to forbs and deciduous shrubs. On the Mount St. Helens blast zone in southwest Washington, Merrill et al. (1995) reported that summer dietary composition was forbs > shrubs > graminoids > ferns, consistent with our findings except that shrubs > forbs. In studies conducted in settings where closed-conifer forests dominated, forbs and grasses were less common in diets, and ferns and conifers were more common (Leslie et al. 1984) than reported by Merrill et al. (1995). Differences among studies undoubtedly reflect differences in availability of plant species that in turn are a function of the mix of successional stages and ecological site conditions among study areas (Merrill et al. 1995). Finally, although elk are often depicted as monocot grazers (Nelson and Leege 1982), we found little overall selection for graminoids, except for sedges and woodrushes (*Carex* spp. and *Luzula* spp.), as did Merrill et al. (1995) in southwestern Washington and Irwin and Peek (1983) in productive red cedar-western hemlock forests in northern Idaho.

Elk selected among plant species based primarily on DE content. The deciduous shrubs and forbs that elk selected were in the plant groups with the highest DE. These species tended to compose high proportions of diets even when their abundance was low. In contrast, elk consumed very few evergreen shrubs and forest ferns, the life-form groups containing the lowest DE and the highest fiber and lignin content (Merrill 1994), unless there was little else to eat, yet these were by far the most abundant and afforded the highest bite mass. Graminoids represented a middle ground; they typically contained relatively high DE, but elk generally consumed them in proportion to their availability.

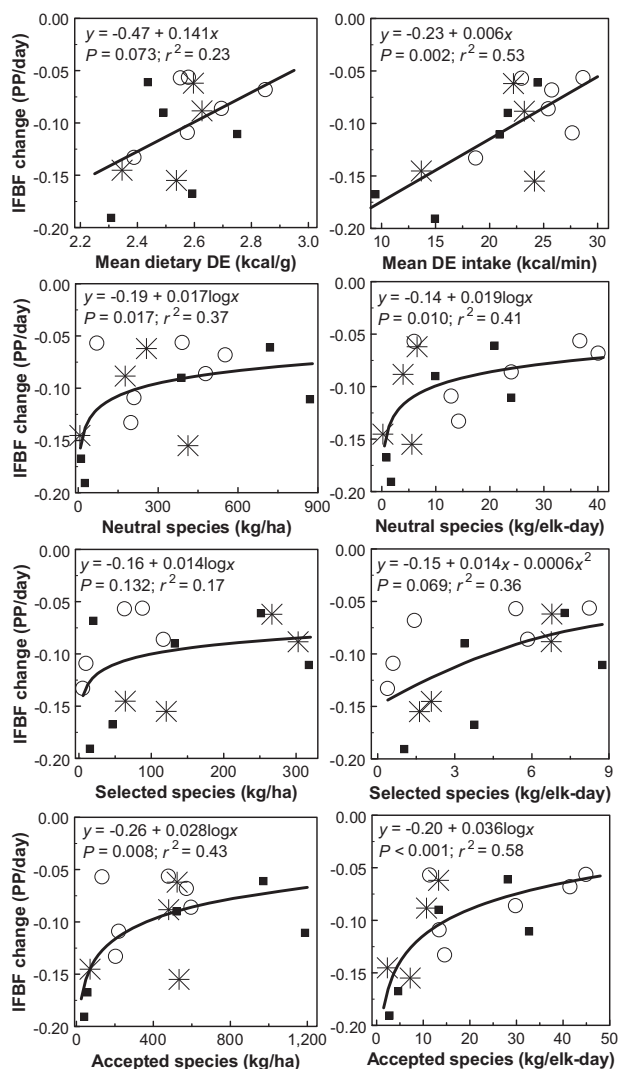


Figure 54. Relations between change in ingesta-free body fat (IFBF), in percentage points (PP) per day, in adult female elk, nutrition variables (dietary digestible energy [DE] and intake rate of DE), and forage abundance variables during foraging trials lasting 13–21 days at 3 study areas in western Oregon and Washington, 2000–2002. Open circles, solid squares, and asterisks represent data collected at the Nooksack, Willapa Hills, and Springfield study areas, respectively.

If elk had foraged at random, it is clear that dietary DE would have been substantially reduced in most plant communities. Thus, selection for plants offering high DE was an effective strategy that helped to maintain relatively high DE across a wide range of AccSpp abundance. Nevertheless, elk failed to maintain high dietary DE as abundance of AccSpp declined <400 kg/ha to 500 kg/ha, generally corresponding to the threshold at which switching to avoided species began (Figs. 36 and 63), at least in the WHS. Because declines in per-minute intake rate of DE occurred when abundance was <200 kg/ha, elk postponed the decline in intake rate of DE by increasing consumption of AvdSpp, although this switching was contingent on high abundance of AvdSpp. This pattern also held for 24-hour intake rates of forage dry matter and DE. In those situations where abundance of AvdSpp and AccSpp combined was low (<500 kg/ha), elk also increased rate of travel while foraging, which helped

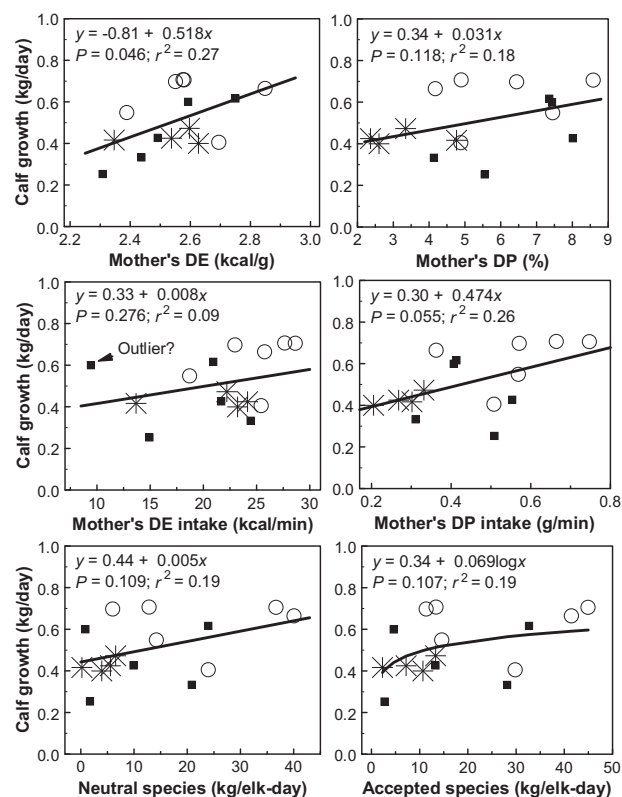


Figure 55. Relations between elk calf growth, dietary digestible energy (DE), DE intake rate, dietary digestible protein (DP), and forage biomass variables during foraging trials lasting 13–21 days at 3 study areas in western Oregon and Washington, 2000–2002. Open circles, solid squares, and asterisks were collected at the Nooksack, Willapa Hills, and Springfield study areas, respectively. The data point marked as a potential outlier is not included in the regression results.

maintain per-minute intake rate, despite lower forage intake per meter traveled (Wickstrom et al. 1984).

Bite mass has a dominant influence on per-minute intake rates (Illius 1997, Shipley 2007), and the wide range of bite mass provided considerable opportunity for elk to increase forage intake rate if they had chosen to consume more low-quality plants. Bite mass is largely a function of mouth size and depth of foraging vertically into vegetation, at least in grassland settings (Illius 1997, Shipley 2007). Larger bites allow greater forage intake rates because fewer bites are required to resupply the mouth (i.e., less time is spent acquiring plant tissue; Spalinger and Hobbs 1992). Mean bite mass ranged 10-fold among pens, from 0.1–1.0 g/bite, similar to that previously reported for elk (Wickstrom et al. 1984, Hudson and Watkins 1986), and ranged 50-fold, from 0.04–2.2 g/bite (Appendix E) among plant species, providing elk with a huge range of bite mass options. However, because elk were selecting among plant species primarily as a function of forage quality, bite mass was largely a response that emerged that was secondary to and secondary to seeking plants of high quality. In mixed communities of shrubs, forbs, and grasses, bite mass is considered a complicated function of plant structure, particularly leaf dimensions and bulk density (Spalinger and Hobbs 1992). Our data indicate that bite mass is additionally influenced by variation in quality among plant species, and that

Table 10. Regression equations of calf growth (kg/day) and change in ingesta-free body fat (IFBF; percentage points/day) as functions of nutrition and forage abundance levels over the multi-day foraging trials for elk at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Length of trials varied from 13 days to 21 days.

Dependent variable	Equation ^a	R^2	R^2_{adj} ^b	$S_{y \cdot x}$ ^b	P
Calf growth	$y = -1.17 + 0.52(DP_{min}) + 0.57(DDE)$	0.58	0.51	0.103	0.006
Calf growth	$y = 0.34 + 0.069(\log TAccSpp)$	0.19	0.18	0.136	0.107
IFBF change	$y = -0.40 + 0.022(date) + 0.005(DE_{min})$	0.66	0.60	0.028	0.002
IFBF change	$y = -0.36 + 0.021(date) + 0.032\log(TAccSpp)$	0.71	0.66	0.026	<0.001

^a Variable names are DP_{min} = mean intake of digestible protein (g) per minute of foraging; DDE = mean dietary digestible energy (kcal/g); TAccSpp = total abundance of accepted species in enclosures at the beginning of the trial divided by number of elk \times number of days of the trial (kg/elk-day); date = date of first day of trial (month + day/31.1); DE_{min} = mean digestible energy (kcal) intake per minute of foraging. All independent variables are individually significant at $P \leq 0.057$ except TAccSpp for the calf growth equation.

^b R^2_{adj} = adjusted coefficient of determination; $S_{y \cdot x}$ = standard error of the estimate.

the influences of this variation in quality on bite mass may exceed the influences of plant architecture on bite mass. Moreover, increasing bite rate is a strategy to compensate for declining bite mass (Spalinger and Hobbs 1992), an effect apparent in summer but not autumn in our study. Even in summer, however, our data suggested a nonlinear upper limit to bite rate set by bite mass that limits the compensatory potential of bite rate (Fig. 28). This curve is virtually identical to that presented for elk by Wickstrom et al. (1984) and is similar to that for elk in grasslands of Alberta (Hudson and Watkins 1986). Thus, because bite rate had modest and inconsistent compensating effects for low bite mass, per-minute dry matter intake generally responded to the interaction of abundances of AvdSpp and AccSpp in the same way as bite mass (Figs. 25 and 46).

We anticipated *a priori* that our estimates of 24-hour forage, DE, and DP intake rates would provide more insights of habitat influences on elk nutrition by accounting for influences of digestive constraints on nutrition better than instantaneous DE intake and dietary DE levels. For example, total daily forage intake was considered to be the single-most relevant nutritional variable relating to animal performance (Minson and Wilson 1994) and was considered superior for ecological evaluations (Fryxell 1991, de Vries and Daleboudt 1994, Wilmshurst et al. 1999, although see Babin et al. 2011). In our data, general patterns of 24-hour DE intake were similar to those of dietary DE levels in respect to habitat type and seral stage (Fig. 51). However, the magnitude of deficiencies indicated by the 24-hour DE intake estimates substantially surpassed that indicated by dietary DE levels in many habitats. Assuming our ability to estimate DE intake over 24-hour periods was reasonably accurate (albeit limited by our sample size of pens where elk were equipped with activity monitors), our findings indicate that assessing nutritional value of plant communities solely based on dietary DE may overestimate nutritional value.

Our findings indicated that elk sacrificed per-minute and particularly 24-hour intake rates of DE to maintain at least moderately high dietary DE, probably for at least 2 reasons. First, avoidance of at least some AvdSpp probably reflected relatively high levels of toxic compounds in those species (Hanley 1997, Launchbaugh et al. 2001). Elk can consume small amounts of toxic plants, but their physiological rate of detoxification must exceed the rate of ingestion of toxins, or the animals are likely to become ill (Robbins et al. 1987a, McArthur et al. 2014). This effect may be important for our study region; in October 2000, we

had 6 sick elk in 3 pens in which elk had virtually nothing to eat except swordfern, salal, Oregon grape, and various conifers, all strongly avoided evergreen species. We suspected elk became ill because they had little choice and consumed these strongly avoided species. We never again placed elk in pens with such complete dominance of these species, and no additional cases of illness occurred through the rest of the study. Elk recovered within 12–24 hours without treatment, suggesting that their illness was due to dietary effects rather than bacterial or viral infection.

Second, it is well-recognized that switching to lower-quality forage increases digestive constraints and reduces digestion rates (Robbins 1983, Weston and Poppi 1987, Grey and Servello 1995, Hobbs 2003, Cook et al. 2004). Although elk can consume large amounts of AvdSpp in short time periods, total retention time in the rumen for digestion is increased by high fiber, lignin, and cell wall content (Spalinger et al. 1986). Hence, a foraging strategy that increases per-minute intake rate by consuming abundant, low-quality species may not increase and may even reduce forage intake over longer periods (Hobbs 2003). For example, Spalinger et al. (1986) showed that disappearance of 80% of highly digestible pea (*Psium sativum*) leaves from the rumen of elk required 2–3 hours, but maple (*Acer saccharum*) leaves and blueberry (*Vaccinium* spp.) stems required 3 \times and 5 \times longer, respectively, for 80% disappearance. For those species in our study with low levels of DE, particularly evergreen species, we would expect that lignin and cell wall content would be higher, and passage rates slower, than even the maple and blueberry plants used by Spalinger et al. (1986). Remains of evergreen shrubs in the rumen 5 days after consumption have been reported for caribou (Bergerud and Russell 1964).

Identifying influences of vegetation would have benefited from a larger sample of 24-hour DE intake data, but 1 aspect is clear: elk could have greatly increased 24-hour DE intake by choosing to consume more abundant, lower-quality forage that offered greater bite mass. The fact that they did not do so suggests elk indeed prioritized maintaining relatively high dietary DE (dietary DE maximizing) over maintaining high DE intake rates (DE intake maximizing). However, a more holistic interpretation is that elk strove to maximize 24-hour DE intake but did so by seeking diets high in dietary DE, relatively low in fiber and lignin, and low in toxic compounds. That is, daily DE intake would have been reduced to an even greater extent if elk

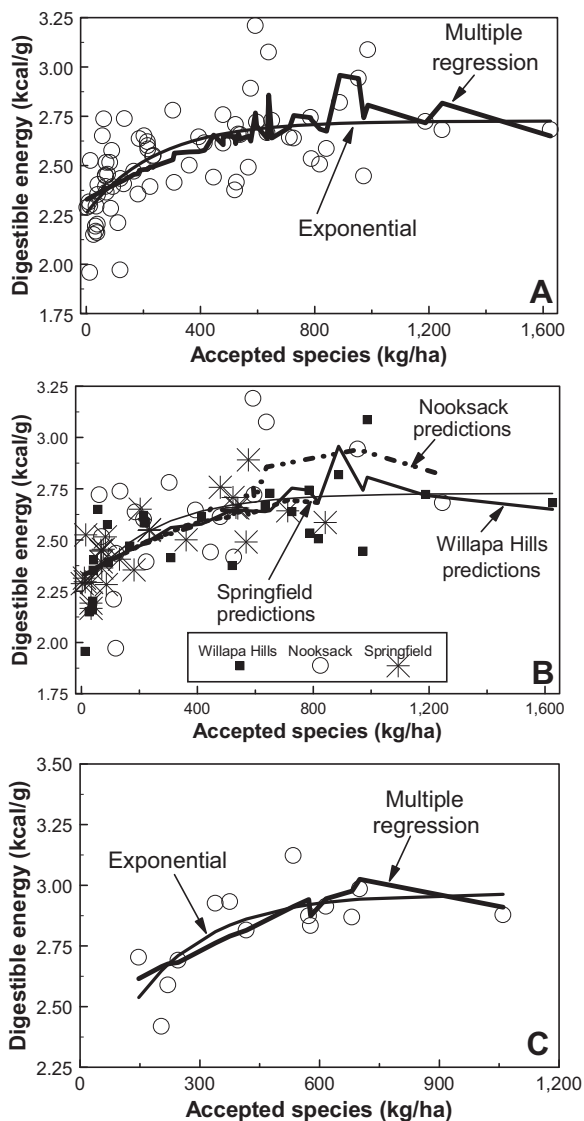


Figure 56. Relations of digestible energy (DE) in elk diets and abundance of accepted forage at 3 study areas in western Oregon and Washington, 2000–2002 (Table 11). In A, plotted lines indicate predictions of DE using an exponential and multiple regression equation, with data from the western hemlock series (WHS) habitat type with all study areas combined. The multiple regression equation includes abundance of neutral and selected plant species as separate independent variables, whereas the exponential equation uses only abundance of accepted species. In B, lines indicate predictions of DE using multiple regression equations developed the WHS habitat type for each study area. The light line is the overall exponential predictions from graph A. In C, lines indicate relations of DE in elk diets and abundance of accepted species in the Pacific silver fir (PSS) and mountain hemlock (MHS) habitat types from all study areas.

had consumed more of the lower quality plants, no matter how rapidly they could consume this forage on a per-minute basis. Thus, high abundance of low-quality food does not compensate for low abundance of high-quality food, even to maximize 24-hour DE intake rates. Daily DE intake rates below requirements in many of the habitat types providing dietary DE above requirements suggests that even some of those plant species that elk readily consumed (AccSpp) modestly reduced daily DE intake. We also suspect that NeuSpp were more likely than SelSpp to reduce intake rate.

Nutritional responses.—Our strongest and biologically most important finding was a functional response between abundance of AccSpp and dietary DE (Figs. 36 and 37). Dietary DE levels began declining below 500 kg/ha of AccSpp and typically ranged <2.6 kcal/g below about 300 kg/ha. These levels negatively affect performance of lactating adults and their offspring (Cook et al. 2004). Explanatory power of this threshold relationship was moderate ($r^2 = 0.49$ – 0.64), but more importantly, the general asymptotic relationship was consistent across seasons (summer and autumn), among the 3 study areas, and between high- (PSS and MHS) and low-elevation (WHS) habitats. Data points that deviated appreciably from the regression line often were from stands with low abundance of AccSpp where elk nevertheless acquired diets relatively high in DE because of a few small patches of palatable and nutritious plant species, or, in several instances, where elk were able to forage predominantly on flowers or berries (Fig. 37, particularly E,F). Elk were effective in locating these patches and plant parts and thus modest exceptions to the general asymptotic pattern are unsurprising.

The linkages among dietary DE, plant succession, and ecological site conditions as reflected in the PNV categories (habitat types) were clear. In the WHS, shade-tolerant evergreen shrubs and ferns nearly completely dominated understory plant communities, and changes in the ratios of these species to those that were more nutritious and palatable occurred only following substantial disturbance. Thereafter, reversion to dominance by unpalatable, shade-tolerant species was very rapid, particularly in the WHS. The greater nutritional value of plant communities in early seral stages than in closed-canopy forests is recognized, but the causal mechanism is often attributed to changes in total forage abundance, rather than changes in species composition and concomitant changes in dietary quality (Gill et al. 1996, Peek et al. 2002).

The functional response between dietary DE and abundance of palatable species has not been reported to our knowledge, although functional responses between per-minute intake rate and forage abundance are well described generally (Spalinger and Hobbs 1992) and specifically for elk (Wickstrom et al. 1984, Hudson and Watkins 1986). Functional response curves may form important links between fine-scale vegetation attributes and important processes of higher order in ecology (Spalinger and Hobbs 1992, van Langevelde et al. 2008). Development of classic concepts of functional responses largely occurred with little consideration of forage quality (van Langevelde et al. 2008). The few exceptions generally involved influences of forage quality on the explicit relation between intake rate and forage abundance, and suggest that lower quality forage dampens the slope of the functional response (e.g., Bergman et al. 2000, Drescher et al. 2006, van Langevelde et al. 2008). But these studies (Bergman et al. 2000, Drescher et al. 2006) used leaf:stem ratios as an index of forage quality in grasslands, markedly different ecological conditions than we encountered. Thus, it is unclear if our dietary DE–AccSpp functional response is a unique feature limited to our ecological setting or if it is a more universal phenomenon.

The observed functional response for dietary DE largely resulted for 3 reasons: 1) 2 quality-palatability categories of forage generally existed, 1 with palatable plant species with relatively high DE and the other with unpalatable species with

Table 11. Equations to predict intake dynamics of dietary digestible energy (DDE) for elk based on abundance (kg/ha) of 3 forage classes in different habitat types and 3 study areas in western Oregon and Washington, 2000–2002.

Equation ^a	<i>n</i>	<i>R</i> ²	<i>R</i> ² _{adj} ^b	<i>S</i> _{<i>y</i>·<i>x</i>} ^b	<i>P</i>
PSS and MHS ^c habitats, all seasons, all study areas					
DDE = 0.944(3.130 – $e^{-0.0055(\text{AccSpp})}$)	14	0.53	na	0.131	0.012
DDE = 2.44 + 0.000889(NeuSpp) + 0.00308(SelSpp) – 0.00000546(SelSpp × NeuSpp)	14	0.56	0.43	0.134	0.036
WHS ^c habitats, all seasons, combined (All) and separately by study area					
DDE _{All} = 0.47 × (5.755 – $e^{-0.0041(\text{AccSpp})}$)	73	0.49		0.174	<0.001
DDE _{All} = 2.32 + 0.000835(NeuSpp) + 0.000829(SelSpp) – 0.00000216(SelSpp × NeuSpp)	73	0.49	0.47	0.171	<0.001
DDE _{Nk} = 2.36 + 0.00108(NeuSpp) + 0.000504(SelSpp) – 0.00000361(SelSpp × NeuSpp)	19	0.49	0.39	0.223	0.015
DDE _{WH} = 2.28 + 0.00062(NeuSpp) + 0.00120(SelSpp) – 0.00000172(SelSpp × NeuSpp)	26	0.52	0.46	0.177	0.001
DDE _{Sp} = 2.30 + 0.00108(NeuSpp) + 0.00129(SelSpp) – 0.00000418(SelSpp × NeuSpp)	28	0.62	0.57	0.115	<0.001
All habitats, all seasons, by study area ^d					
DE _{min} = Int ^e + 0.004(AvdSpp) + 0.026(AccSpp) – 0.0000070(AvdSpp × AccSpp) – 0.000010 (AccSpp ²) – 1.56 (date) + 4.041(Thnd) ^f	89	0.43	0.37	6.57	<0.001

^a Dependent variables for the 3 study areas, Nooksack (Nk), Willapa Hills (WH), and Springfield (Sp), are DDE = dietary digestible energy (kcal/g of forage consumed); DE_{min} = intake of digestible energy/minute of foraging (kcal/min). Forage class codes used as independent variables are NeuSpp = abundance (kg/ha) of neutral plant species, SelSpp = abundance (kg/ha) of selected plant species, AvdSpp = abundance (kg/ha) of avoided plant species, AccSpp = abundance (kg/ha) of accepted species (SelSpp and NeuSpp combined).

^b *R*²_{adj} = adjusted coefficient of determination; *S*_{*y*·*x*} = standard error of the estimate.

^c Habitat codes are PSS = Pacific silver fir series; MHS = mountain hemlock series; WHS = western hemlock series.

^d Equations were separated by study area based on significant dummy variables representing each study area, but coefficients for all other terms were identical for each study area.

^e Int = intercept, which is 28.0 if study area is Nooksack, 23.1 if the study area is Willapa Hills, and 23.0 if the study area is Springfield.

^f Thnd is a dummy variable that is 1 if the stand was thinned and 0 if it was unthinned.

relatively low DE; 2) many plant communities provided almost entirely only unpalatable, low-quality forage; and 3) elk increased consumption of the unpalatable, low-quality plants in those communities where AccSpp were rare, and strong declines in dietary DE occurred. In our setting, disturbance and forest succession largely dictated the relative abundance of the 2 categories of forage. Where succession or ecological conditions have less influence on species composition, the DE functional response we identified may be less apparent, and functional responses between forage abundance and forage intake rate may be more likely.

The relatively weak and inconsistent functional responses we found between abundance of AccSpp and per-minute forage intake rate contrasted sharply with those reported by Wickstrom et al. (1984) and Hudson and Watkins (1986). Both studies reported asymptotic thresholds for forage intake rates at about

1,000 kg/ha, whereas we documented just 200 kg/ha. However, the functional responses described by Wickstrom et al. (1984) and Hudson and Watkins (1986) were for simple pastures and grasslands. This relationship either changed considerably (asymptote at lower levels of forage abundance; Wickstrom et al. 1984) or disappeared altogether (Hudson and Watkins 1986) for data collected in forested communities. Because of the dominant influence of bite mass on instantaneous intake rate (Illius 1997, Shipley 2007), we expect that the functional response in grasslands was due to declining bite mass as total forage declined. Because of the complicating influences of plant architecture (Spalinger and Hobbs 1992) and variable forage quality among plant species in mixed communities of shrubs, forbs, and grasses, no meaningful relationships may exist between forage quantity and intake rate. Hence, in ecological settings where overall food quality is high relative to animal requirements

Table 12. Equations to predict dietary digestible protein (DDP) intake dynamics for elk based on abundance (kg/ha) of selected forage classes and other habitat variables at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. We present 2 forms of the equations, 1 that included wet site indicators and the other that included plant life-form groups.

Equation ^a	<i>n</i> ^b	<i>R</i> ²	<i>R</i> ² _{adj} ^c	<i>S</i> _{<i>y</i>·<i>x</i>} ^c	<i>P</i>
DDP = Int ^d + 0.0088(logAccSpp × CC) + 1.88(Habt) ^e + 34.9(Wetp) – 0.294(Wetp × CC) – 0.63(Date) ^f	88	0.59	0.56	1.77	<0.001
DDP = 10.8 + 0.0091(logAccSpp × CC) + 1.59(Habt) ^e + 0.0025(Ffrn) – 0.000025(Ffrn × CC) – 0.374(logEshr) – 0.69 (Date) ^f	88	0.61	0.58	1.72	<0.001
DP _{min} = 0.85 + 0.001(logAccSpp × CC) + 0.113(Habt) ^e + 1.436(Wetp) – 0.000042(CC ²) – 0.067(Date) ^f + 0.125(Thnd) ^g	88	0.45	0.41	0.198	<0.001
DP _{min} = 1.09 + 0.0010(logAccSpp × CC) + 0.162(Thnd) ^g – 0.029(logEshr) – 0.000035(CC ²) – 0.072(Date) ^f	88	0.45	0.42	0.196	<0.001

^a Dependent variables are DDP = dietary digestible protein (% of forage dry matter consumed); DP_{min} = intake of digestible protein/minute of foraging. Forage class codes used as independent variables are AccSpp = abundance (kg/ha) of accepted species, Eshr = abundance (kg/ha) of evergreen shrubs; Ffrn = abundance (kg/ha) of shade tolerant ferns; Wetp = the combined abundance of swordfern, red alder, ladyfern, and salmonberry, wet site indicators in western Oregon and Washington, expressed as a proportion of total understory abundance. CC = overstory canopy cover (%).

^b Sample size was 88 because overstory measurements (CC) were not collected at 1 pen.

^c *R*²_{adj} = adjusted coefficient of determination; *S*_{*y*·*x*} = standard error of the estimate.

^d Int = intercept, which is 8.49 if study area is Nooksack or Willapa Hills or 7.68 if the study area is Springfield.

^e Habt is a dummy variable that is 1 if the site was located in either Pacific silver fir or mountain hemlock habitats and 0 if it was located in western hemlock habitats.

^f Date are calculated as month + (day/31.1).

^g Thnd is a dummy variable that is 1 if the stand was thinned and 0 if it was unthinned.

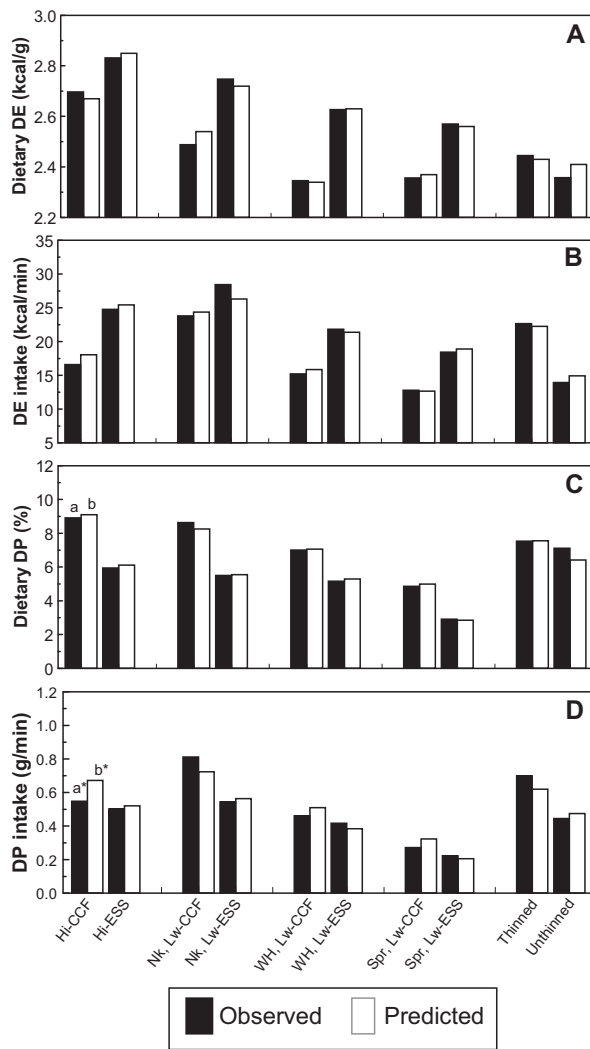


Figure 57. Means of predicted and observed dietary digestible energy (DE; A), DE intake rate (B), dietary digestible protein (DP; C), and DP intake rate (D) for adult female elk by categories of habitat type, successional stage, and thinning among the Nooksack (Nk), Willapa Hills (WH), and Springfield (Spr) study areas in western Oregon and Washington, 2000–2002 ($n = 89$ macroplots). Codes are Hi = Pacific silver fir (PSS) and mountain hemlock (MHS) habitats at high elevations, Lw = western hemlock (WHS) habitats at low elevations; CCF = closed-canopy forests; ESS = early seral stages; thinned = thinned stands; and unthinned = unthinned stands. Comparisons of thinned and unthinned were limited to stands in WHS ranging in age from 20 years to 60 years. Within habitat type, successional stage, study area, and thinning categories, predicted bars with different letters than the observed bars indicate significant differences ($P \leq 0.05$ or $0.05 < P \leq 0.10$ if *). Predicted values were derived from DE and DP equations in Tables 11 and 12.

and plant architecture is relatively simple, classic functional responses between forage, DE, and nutrient intake rates and forage abundance may be strong. Otherwise, such relationships may be weak.

We were limited in separating the influences of changing species composition versus changing solar flux and soil moisture dynamics on nutritional value of plant communities as succession advanced. In general, higher levels of sunlight favor higher levels of sugars and other cell solubles in plants, and DE levels respond accordingly (Blair et al. 1983, Van Soest 1994), although the opposite evidently occurs for crude protein (Blair et al. 1983).

Hanley et al. (1987), Van Horne et al. (1988), and Happe et al. (1990) found in western Washington that under conditions of high moisture and full sunlight, such as in clearcuts, defensive compounds (mainly tannins) that can reduce forage digestibility and available protein may be elevated and reduce the nutritional value of forage. Hence, they suggested that despite the greater abundance of forage in early seral stages, greater nutritional value may exist in closed-canopy forests, at least for deer. By including tannin astringency, the studies of Hanley et al. (1987), Van Horne et al. (1988), and Happe et al. (1990) may more completely quantify DP levels of forage for our ecological setting. However, comparing tannin astringency among a limited number of species growing inside and out of clearcuts may incompletely describe clearcutting effects on nutritional value for elk. Working in the Mount St. Helens blast zone, Merrill (1994) indicated that the differences in abundance of relatively nutritious plants and highly lignified, low-quality plants in early seral versus closed-canopy forests may strongly influence nutritional value of plant communities to elk.

Differences in tannin astringency levels in our elk diets across the successional sequence were relatively minor, although tannin astringency was modestly elevated in 12–20-year-old stands with overstory canopy cover of 40–70% (Figs. 31 and 32). We also found little evidence of seasonal, habitat type, or thinning effects. One explanation for these results is that many plant species that elk readily consumed in clearcuts did not contain tannins (e.g., grasses, sedges, lichen, species in the Asteraceae and Liliaceae; Cook 2002). Moreover, development of woody species in clearcuts was rapid, so plants of low stature were substantially shaded, particularly >3 growing seasons after the final herbicide application. Elk had substantial opportunities to select plants and obtain diets with low levels of tannin astringency (McArthur et al. 1993), and thus dietary tannin astringency in clearcuts was evidently a minor issue.

Finally, dietary DP seemed invariant to forage selection patterns of our elk and exhibited little relationship with forest succession. We expected that dietary DP would be correlated with dietary DE, such that succession and ecological site conditions that influenced DE would similarly affect DP. But neither was correlated. Dietary DP was elevated in pens with greater soil moisture, higher in pens with greater canopy cover, declined with season, was higher in thinned stands, and was higher in alder-dominated hardwood stands, all generally in contrast to patterns apparent for dietary DE. All the analyses we present herein for dietary DP also were initially conducted for dietary crude protein, and the results were virtually identical. Thus, the ecological patterns we found for dietary DP did not result from incorporating effects of tannin astringency to calculate DP. Finally, the estimates of DP intake per minute and per 24 hours in relation to the abundance of our forage selection categories also were imprecise and seemingly illogical.

The performance trials involving measures of body fat and calf growth dynamics were designed to confirm that 1) relations between DE nutrition and performance from controlled experiments using artificial rations (Cook et al. 2004) generally held for elk consuming native vegetation; and 2) vegetation attributes that were related to nutrition of elk also were related to their performance. Dietary DE levels and per-minute DE intake rates

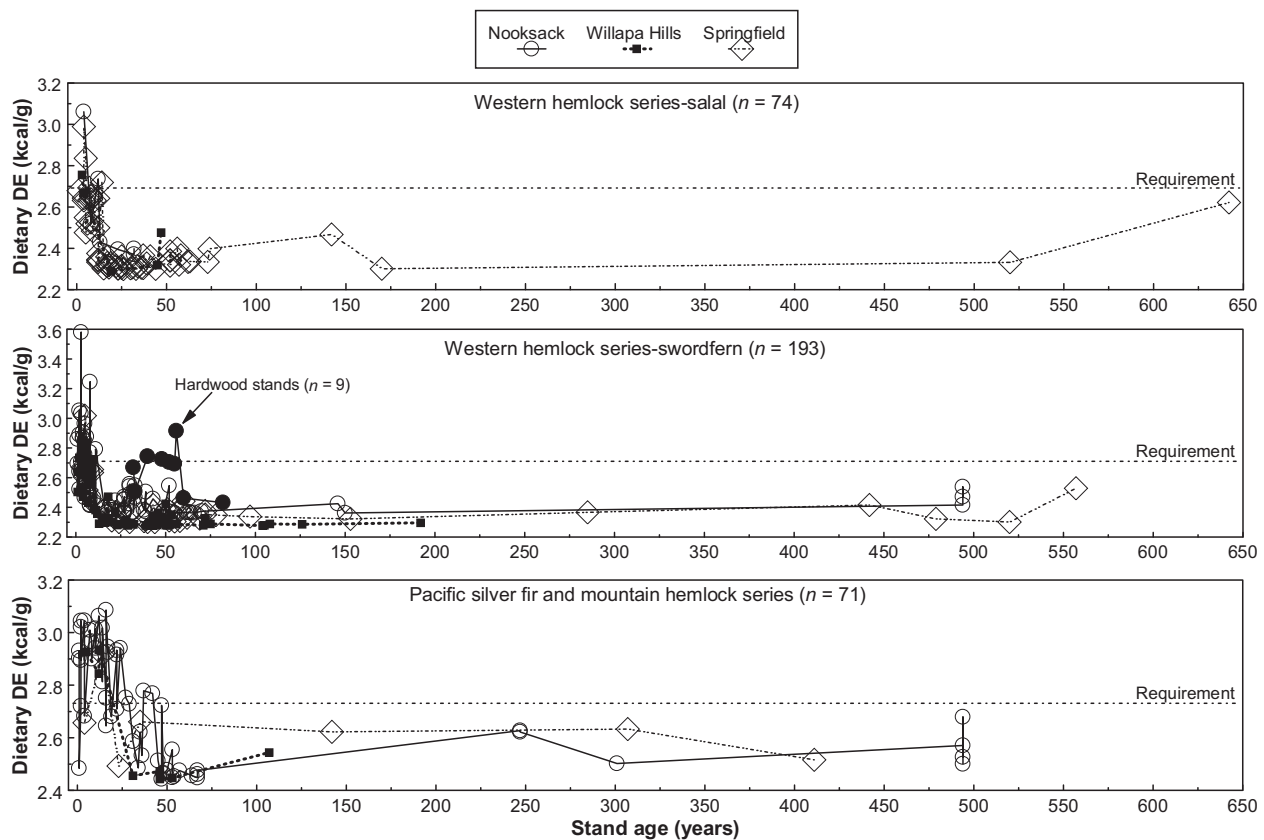


Figure 58. Estimates of dietary digestible energy (DE) for adult female elk (calculated from equations in Table 11) by study area and habitat type across succession at 3 study areas in western Oregon and Washington, 2000–2002. The horizontal requirement line indicates DE levels needed by lactating female elk to hold constant body fat levels in summer.

were below requirements of lactating elk in summer in all but 2 pens and adult elk were unable to increase body fat levels in any of the 15 pens. This finding generally matches *a priori* expectations derived from controlled experiments using artificial rations (Cook et al. 2004).

The experiments also confirmed the importance of abundance of AccSpp in driving animal performance. Rate of body fat loss of the lactating females was correlated to their DE intake rate over the course of the experiments and was nonlinearly related to abundance of AccSpp in the pens at the beginning of the trial (Fig. 54). Declines in body fat greatly accelerated in pens with <400 kg/ha of AccSpp, consistent with our threshold for dietary DE levels, but we found little evidence of an asymptote in body fat change as a function of the abundance of AccSpp. This absence of an asymptote suggests that our forage abundance thresholds for short-term dietary DE and DE intake rates (400–500 kg/ha and 200 kg/ha, respectively) based on our foraging trials may be too conservative in the context of performance of lactating elk.

Calf growth responses to nutrition of their mothers and abundance of AccSpp provided similar conclusions; in pens where maternal DE intake was greater, calf growth was higher as well, although the relation between abundance of AccSpp and calf growth was not significant. Growth of elk calves is highly related to their DE intake (Cook et al. 1996), which we did not measure, so we used maternal nutrition as an index of calf

nutrition. The calf data were complicated by several attributes of the study. Calves grew more rapidly as the summer progressed, regardless of their mother's nutrition, probably because calves became less dependent on milk from their mothers after midsummer. In addition, calves often exited the pens and consumed forage that was unavailable to their mothers. Thus, nutritional inputs for calf growth varied increasingly as summer progressed, and probably introduced some unexplained variation in our calf growth data.

Growth rate of calves averaged about 0.5 kg/day, about half the level at which elk calves are capable if nutrition in summer is not limiting (Robbins et al. 1981, Hudson and Adamczewski 1990, Cook et al. 1996), supporting the conclusion that the nutritional environment in most of the pens was strongly limiting. Calf growth and adult body fat trends did differ in one respect: growth also was weakly correlated to maternal intake rate of DP. Dietary DE has strong effects on growth of juvenile ungulates (Holter and Hayes, 1977; Cook et al. 1996, 2004), to a greater extent than protein (Verme and Ozoga 1980), but rapid growth of muscles and organs likely creates a higher mass-specific nitrogen demand in juveniles than would be expected for adult females (Cook 2002, Hudson and Haigh 2002).

Summer Nutritional Limitations for Wild Elk Herds

Our data strongly suggest important causal links between nutrition levels in plant communities we sampled and the

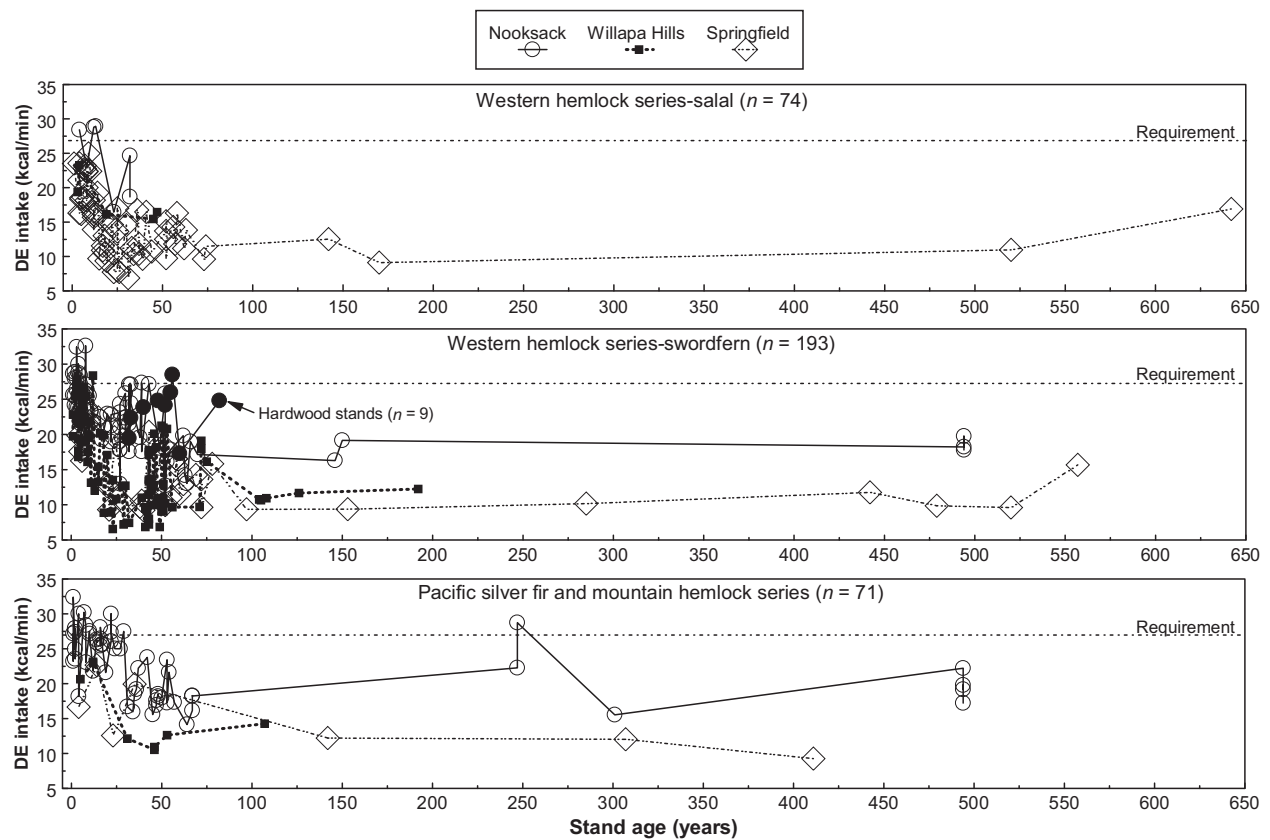


Figure 59. Estimates of digestible energy (DE) intake/minute of foraging by adult female elk (calculated from equations in Table 11) by study area and habitat type during succession at 3 study areas in western Oregon and Washington, 2000–2002. The horizontal requirement line indicates DE intake levels needed by lactating female elk to hold constant body fat levels in summer (assuming feeding time of 13 hr/day).

relatively low pregnancy rates and autumn body fat levels of elk in the region (Trainer 1971, Kuttel 1975: 17, Smith 1980, Harper 1987: 12, Stussy 1993, Cook et al. 2013). Early seral forests that support dietary DE levels that satisfied requirements were highly ephemeral, lasting only 10–15 years in forests at low to moderate elevations and 20–45 years at high elevations across the successional sequence. On intensively managed industrial and state-owned timberlands where timber harvest rotations occur at 40- to 60-year intervals, this early seral vegetation can be expected to average as low as 20% of landscapes over time, particularly in the WHS. Largely as a result of the Northwest Forest Plan (U.S. Department of Agriculture Forest Service and U.S. Department of the Interior Bureau of Land Management 1994a, b), timber harvest has been nearly eliminated on federal public lands since the early 1990s (Oregon Department of Fish and Wildlife 2008). Swanson et al. (2014) suggested that natural early seral forests already may be among the rarest habitats in the Pacific Northwest. Wild elk that depend on managed and particularly unmanaged wildlands may be increasingly challenged to acquire DE nutrition levels that satisfy requirements in many areas.

Selection by elk for habitats that provide good nutrition via elevational migration and within summer home ranges is potentially a powerful mechanism through which elk might mitigate for overall poor nutritional resources available to them. At least in the Cascades Mountains, many elk herds should have the opportunity to migrate in summer to higher elevations

that provide better nutrition (Hebblewhite et al. 2008). Some migrate, but many do not (Cook et al. 2013, Geary 2014). In contrast, elk in summer exhibit strong selection for habitats offering relatively good nutritional value in the Pacific Northwest (J. Cook and R. Cook, National Council for Air and Stream Improvement, unpublished data), but the prevalence of depressed autumn body fat and pregnancy rates in the Pacific Northwest suggest that such selection generally fails to compensate for landscapes that offer relatively poor nutritional resources.

Cook et al. (2013) described 2 regional gradients of body fat and pregnancy, a north-south gradient on the west-slope of the Cascades extending from the Canadian border nearly to the California border in southwest Oregon (higher levels in the north), and an east-west gradient extending from the Cascades crest to the Pacific Ocean (higher in the east). Our foraging data from 3 of the 12 herd ranges sampled by Cook et al. (2013) are consistent with these regional gradients in body fat and pregnancy. We found better nutritional resources at Nooksack than at either Willapa Hills or Springfield, probably a product of the greater prevalence of high-elevation habitats (PSS and MHS) and the northerly latitudes there. This result is consistent with the significantly greater autumn body fat levels and pregnancy rates at Nooksack than the other 2 areas (Cook et al. 2013). In fact, body fat levels of elk at Nooksack were the highest documented among 21 herds in Washington, Oregon, and the Rocky Mountains (Cook et al. 2013).

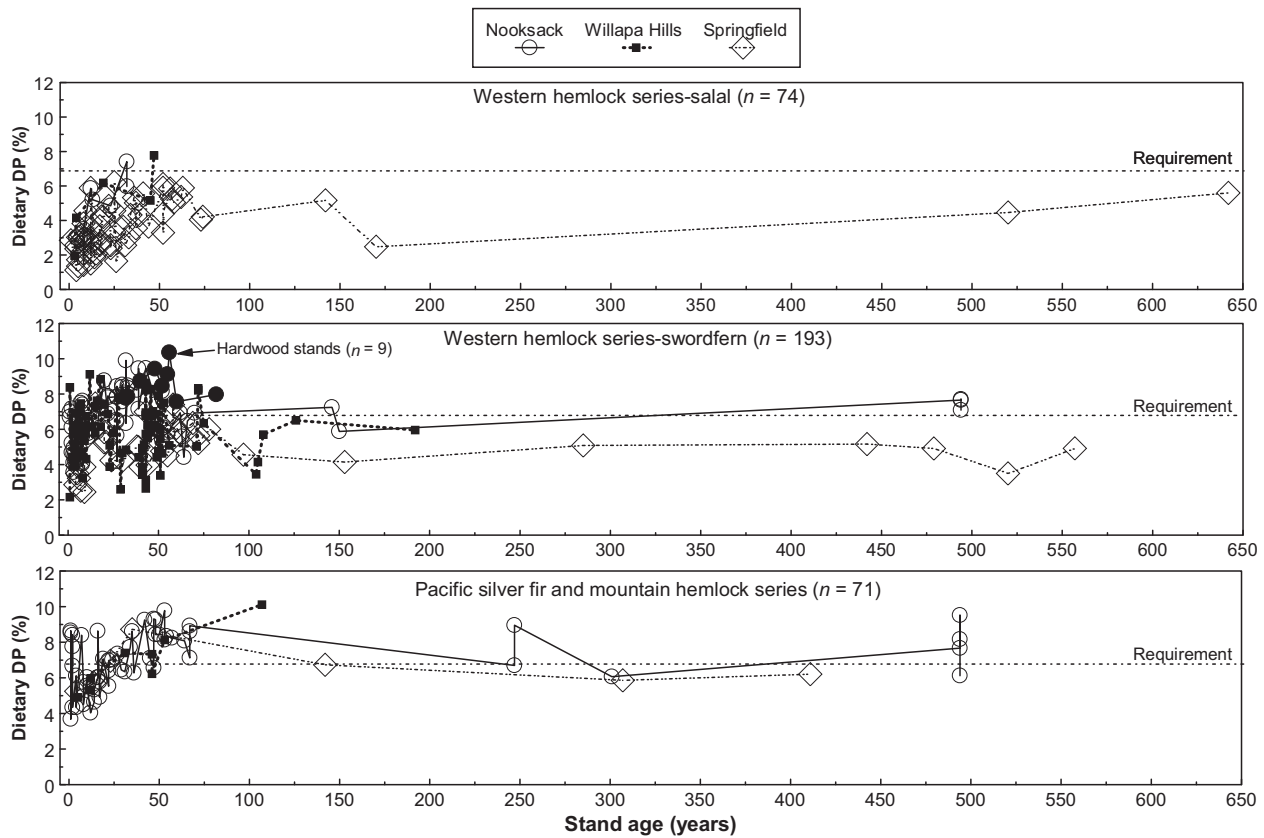


Figure 60. Estimates of dietary digestible protein (DP) for adult female elk (calculated from equations in Table 12) by study area and habitat type across succession at 3 study areas in western Oregon and Washington, 2000–2002. The horizontal requirement line indicates DP levels needed by a lactating female elk in summer.

Thus, our data suggest that influences of ecological site conditions and forest succession on nutritional value at fine scales influence higher-order processes of elk populations across landscapes. Natural, large-scale disturbances that created enormous areas of early seral vegetation dramatically increased density and productivity of ungulate herds in the region, including black-tailed deer in response to the Tillamook burns in the 1930s (Einarsen 1946) and elk on the Mount St. Helens blast zone (Merrill 1987). Forest management that creates early seral stages also benefits wild herds. In the Olympic Peninsula in western Washington, Hutchins (2006) reported depressed calf:cow ratios (i.e., <0.3) in areas with relatively few stands of early seral communities and significantly greater ratios in areas with more early seral communities created by active forest management.

Nevertheless, alternative hypotheses might explain the low levels of body fat and pregnancy observed in the region. For example, winter weather and nutrition have been long believed to be responsible for depressed nutritional condition, reproduction, and survival (Wallmo et al. 1977, Houston 1982, Skogland 1990, Christensen et al. 1993, Coughenour and Singer 1996). However, winter weather on most elk winter ranges in the Pacific Northwest was relatively mild; elk rarely encountered appreciable snow, particularly in the coastal area of western Oregon and Washington where autumn body fat and pregnancy rates were most depressed (Stussy 1993, Cook et al. 2013). Certainly, loss of nutritional condition over winter is ubiquitous

in the western United States including on the relatively mild winter ranges of the Pacific Northwest, but nutritional condition in early spring is primarily a function of nutritional condition the previous autumn (Cook et al. 2013). Nutritional condition in autumn and spring, pregnancy rate, and most other life processes related to population performance are a direct function of nutrition during summer, not the previous winter (Cook et al. 2004, 2013). Others also have attributed low autumn body fat and pregnancy rates to limiting effects of summer nutrition in our study region (Trainer 1971, Harper 1987), and the importance of summer and early autumn nutrition is garnering considerable support for ungulates worldwide (Cr  te and Huot 1993, Hjeljord and Histol 1999, Dale et al. 2008, Cook et al. 2013, Hurley et al. 2014). Therefore, we posit that summer nutrition has strong influences on annual cycles of nutritional condition and most key life processes that may override winter influences in our study region (Cook et al. 2013).

A second alternative hypothesis is that nutritional condition and pregnancy rates may be depressed by human disturbance (Davidson et al. 2012) and predators (Creel et al. 2007), which may increase daily movements, displace elk from nutritionally superior habitats, and disrupt normal feeding patterns. Much has been written regarding the deleterious effects of fear on elk (Creel et al. 2005, 2007, 2011) largely based on research in Yellowstone National Park, but subsequent work in that ecosystem has failed to confirm those inferences of predator effects on nutritional condition, pregnancy rate, movements, and habitat use (White

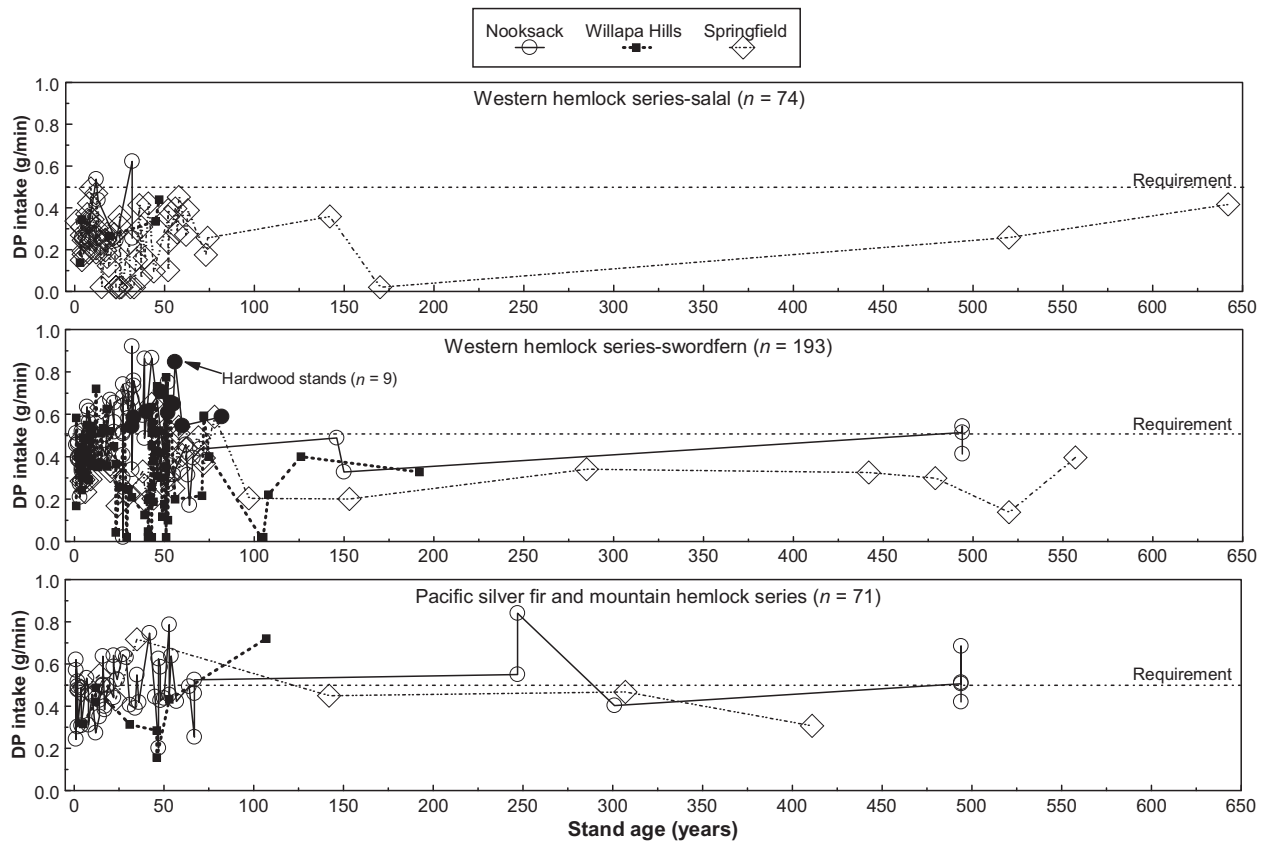


Figure 61. Estimates of digestible energy (DE) intake/minute of foraging by adult female elk (calculated from equations in Table 12) by study area and habitat type across succession at 3 study areas in western Oregon and Washington, 2000–2002. The horizontal requirement line indicates DE intake levels needed by lactating female elk in summer (assuming feeding time of 13 hr/day).

et al. 2009, Kauffman et al. 2010, White et al. 2011, Boonstra 2013, Middleton et al. 2013a, b). Wolves (*Canis lupus*) were not present in our study region, but cougars (*Felix concolor*) and black bears (*Ursus americanus*) were common in most herd ranges, predation on elk neonates was high for some, and hunting occurred for most herds evaluated by Cook et al. (2013). If we had found that the nutritional value of most of the habitats in our study areas satisfied requirements to support relatively high levels of nutritional condition, pregnancy rates, and juvenile growth and development, then our results would provide some implicit support for the hypothesis that the ecology of fear was responsible for low body condition and pregnancy rate. But they do not.

Finally, our data did not account for foraging effects and density of extant elk on our study areas; the low levels of dietary and intake rate of DE we observed could have been the result of long-term selective removal of high-quality forage from plant communities in our study (Riggs et al. 2000), and elk density, relative to carrying capacity, could have accounted for variation in nutritional condition and reproduction in the region's elk herds. However, vegetation in the Pacific Northwest is among the most productive on the planet (Franklin and Dyrness 1988), and simple calculations show that elk herds on our study areas consumed only a small percentage of understory vegetation (roughly 0.5% from mid-spring through mid-autumn assuming 0.5 elk/km², the approximate density of elk at Nooksack and Springfield [see study area description]). We cannot prove that

our estimates of elk nutrition were uninfluenced by herbivory effects of extant elk on plant communities, but our data clearly illustrated dominant influences of ecological site conditions and forest succession on elk nutrition.

We postulate that density-independent nutritional limitations may play an important role linking habitat attributes and elk productivity in our region. The concept of density-dependent, inverse relations between herbivore numbers and abundance of vegetation (Caughley 1979, McCullough 1984, Fowler 1987) serves as a cornerstone of large ungulate management in North America. Important limitations of inadequate food supply on populations are believed to occur mainly as populations approach carrying capacity, where carrying capacity is defined as the maximum number of animals that can be supported (i.e., ecological carrying capacity; Caughley 1979), not when herbivore density is well below carrying capacity (Skogland 1986, Fowler 1987), in turn suggesting that low pregnancy rates and body fat are, in fact, indicative of populations at or near carrying capacity. However, development of the concept largely occurred in the absence of data on forage quality (DeYoung et al. 2008), and density dependence is increasingly being challenged. In settings where the majority of forage is of low quality (Shea et al. 1992, Shea and Osborne 1995, Crête and Courtois 1997) or where quality of nutritional resource varies greatly among years (DeYoung et al. 2008), relatively low levels of performance may occur at ungulate densities well below carrying capacity, and

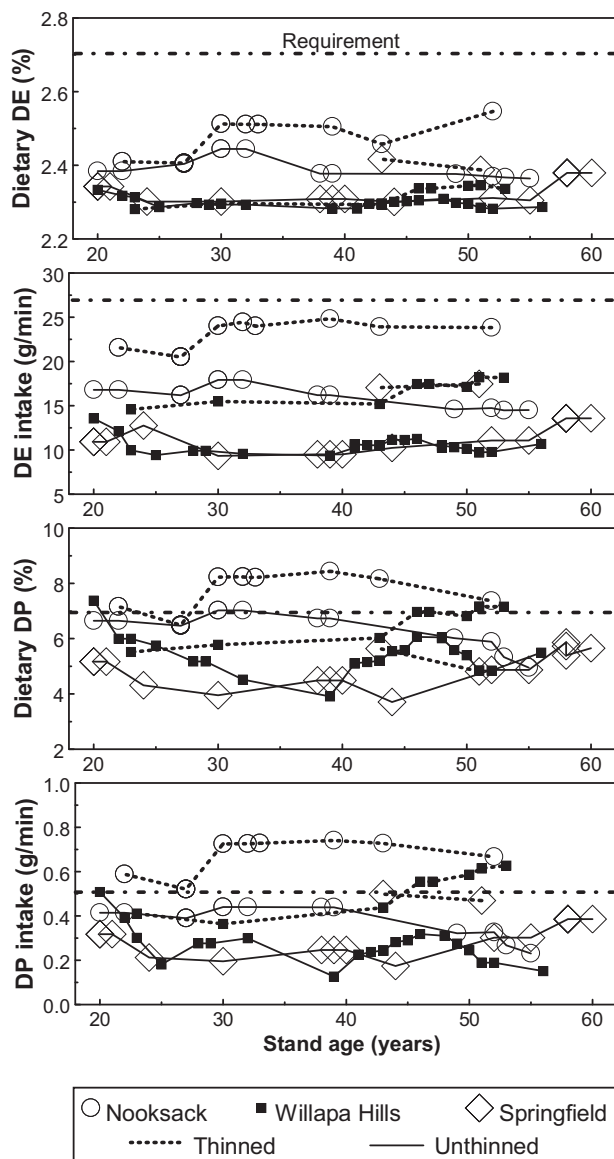


Figure 62. Estimates of digestible energy (DE) and digestible protein (DP) of elk (calculated from equations in Tables 11 and 12) in thinned and unthinned mid-seral forests in western hemlock (WHS) habitats by study area in western Oregon and Washington, 2000–2002. Plotted data values are 5-year moving averages. Horizontal requirement lines represent levels required by lactating female elk in summer.

density dependence may have limited practical management implications (Mackie et al. 1990, McCullough 1999, DeYoung et al. 2008, and see Krebs 2002 and Berryman et al. 2002).

Hobbs and Swift (1985) provided a relatively comprehensive and compelling strategy to integrate forage quality and quantity. In general, the amount of forage at different levels of forage quality, particularly the amount that satisfies nutritional requirements, serves as the foundation of their approach. Hobbs and Swift (1985) described 2 extremes in the context of interrelationships among forage quality, quantity, and herbivore density: those habitats that provide high-quality forage at low levels of biomass and those that provide low-quality forage at high levels of biomass. The former would be expected to support productive populations that exist on high-quality diets but only at low

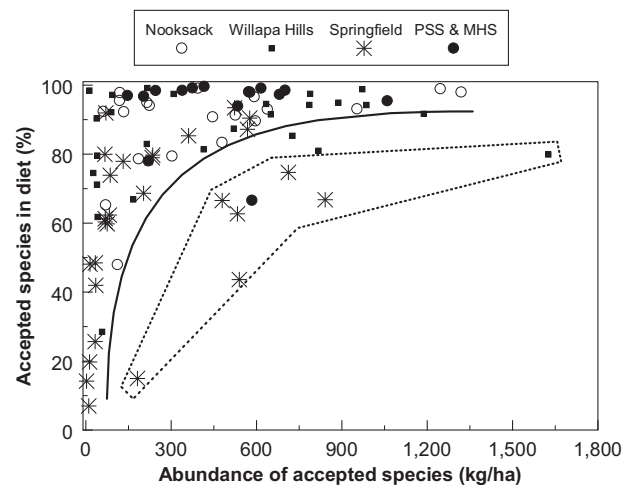


Figure 63. Proportion of diets of accepted plant species in relation to the abundance of accepted species available in each elk pen in all habitat types at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Estimates inside the polygon (dotted line) were from either the first or second pen sampled the first year we used elk in the study at Springfield and the first pen sampled the second year (Willapa Hills), suggesting that elk were more willing to consume avoided species very early in the study. PSS = Pacific silver fir series; MHS = mountain hemlock series.

density, and the latter would support relatively unproductive populations but potentially at high density. Density-dependent and -independent nutritional influences on animal productivity and population growth may vary among these extremes and perhaps other forage quality-quantity combinations.

Our data suggest at least 3 nutritional settings in our region where density-independent and density-dependent influences may differ (Fig. 64). The first setting may be landscapes primarily composed of mid and late seral stages in forests at low to moderate elevation, where forage quality is low but total forage is reasonably abundant. At very low elk density, the few elk present could locate and exploit small patches of high-quality forage and thus their nutrition, body fat, and pregnancy would be reasonably high. But elevated productivity would disappear with only slight increases in density as these patches were exploited. Because total forage is abundant, the landscape might support substantially greater density of elk. However, productivity and growth of these elk populations would be depressed and largely invariant across a wide range of density (Fig. 64). Certainly, density-dependent influences would be expressed near carrying capacity, but populations would be very slow to achieve carrying capacity because of density-independent limitations on reproduction and survival imposed by ecological constraints, not density-dependent influences, that hold forage quality at low levels. In this setting, density-dependent limitations would be of little practical relevance (McCullough 1999). A key management implication of this is that population reductions intended to increase *per capita* nutrient availability might largely fail to improve elk productivity.

A second setting where density-independent and density-dependent influences may differ is on landscapes supporting mid and late seral forests at high elevations, where forage abundance would be low but a greater proportion of forage may be of high quality. Here, populations may be productive as long as density is modest (Hobbs and Swift 1985) but might rapidly decline as

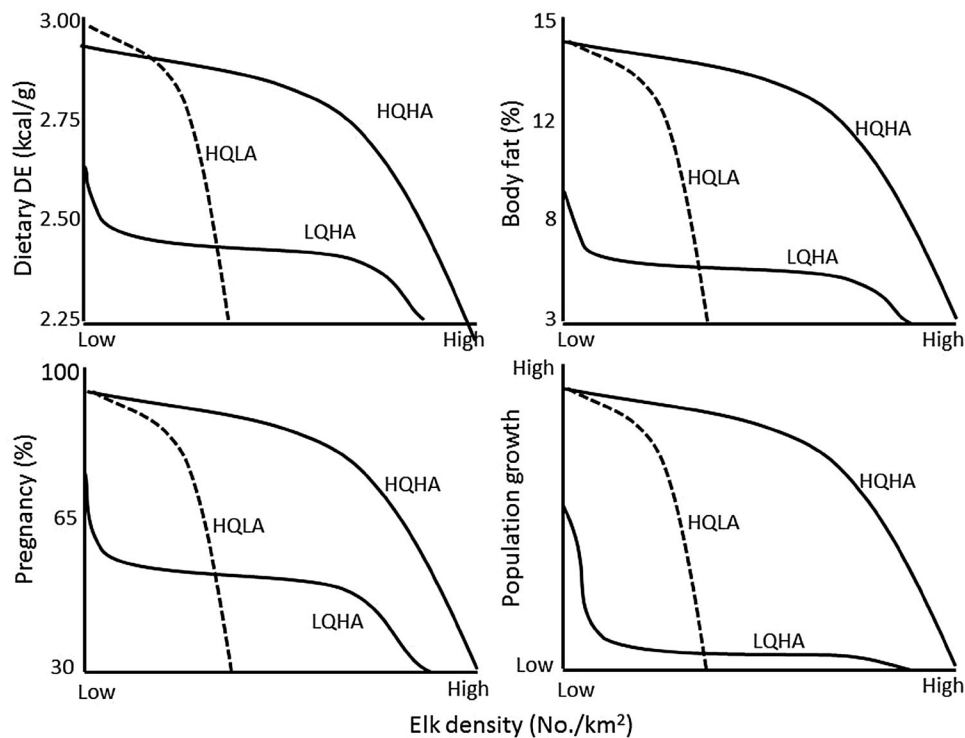


Figure 64. Hypothetical relationships among elk density and dietary digestible energy (DE) in summer and early autumn, autumn body fat, pregnancy, and potential population growth among 3 landscape types offering 1) high-quality, abundant forage (HQHA); 2) low-quality, abundant forage (LQHA); and 3) high-quality, sparse forage (HQLA).

populations build. Thus, density-dependent restrictions might be very strong, and density-independent limitations inconsequential, across a relatively narrow range of density. Finally, on landscapes supporting predominantly early seral forests at higher elevations, forage abundance and quality would be high, and these landscapes would be able to support productive populations across a wide range of densities (Fig. 64), and, again, density-independent influences would be of little consequence over any range of elk density. Landscapes at high elevations where forest overstories were removed by the eruption of Mount St. Helens in Southwest Washington (Merrill 1987) may initially represent this high-quality, high-forage-biomass setting, although the rapid rate of succession evidently has returned much of this area to mid seral forests (Washington Department of Wildlife 2006). The setting of low-quality, abundant total forage, where influences of density independence predominate, may nevertheless best describe many landscapes in western Oregon and Washington. Whatever the case, our data clearly identify the strong influences of soils, climate, disturbance regime, and succession on nutritional value of plant communities, influences that have direct relevance to elk productivity. These likely have little relation to extant herbivory, and thus we postulate that nutritional limitations in the region are at least in part due to density-independent influences. Considerably better estimates of herbivore densities and different research designs are necessary to separate density-dependent and -independent influences.

Nutrition in Habitat Evaluation and Landscape Planning

Approaches accounting for nutritional influences for habitat and landscape evaluation historically are varied and, remarkably,

unsupported with rigorous validation. Perhaps foremost among these for elk were habitat evaluation models (Leege 1984, Lyon et al. 1985, Thomas et al. 1988, Wisdom et al. 1986), the tools of choice for landscape planning across millions of hectares of federal public lands. These either ignored nutrition or attempted to address nutrition without explicit accounting for forage quality (Edge et al. 1990). Conceptually a step forward, models developed using correlative resource selection function (RSF) analyses (Boyce et al. 2002, Manly et al. 2002) better account for heterogeneity of habitat by being spatially explicit and by integrating influences of multiple covariates with different currencies (e.g., food, cover, safety) that affect animal distributions and population performance (Boyce et al. 2002).

Early carrying-capacity models attempted to explicitly quantify nutritional resources but were in essence simple, spatially inexplicit mechanistic models. These initially focused on forage abundance, and versions soon followed that measured supplies of nutrients (i.e., forage amount \times nutrient levels in the forage, to estimate kg of protein/ha or kcal of DE/ha), an approach subsequently shown to be flawed for ruminant herbivores (Hobbs and Swift 1985). The carrying capacity algorithm of Hobbs and Swift (1985) and Hanley et al. (2012) improved on this approach by estimating abundance of forage that satisfies animal nutritional requirements. Finally, complex mechanistic models began to appear by the early 1990s (Turner et al. 1994, Coughenour and Singer 1996, Moen et al. 1997, Farnsworth and Beecham 1999, Morales et al. 2005), many of which attempted to account for spatial and temporal heterogeneity in nutritional resources, animal choice for resources, and linkages between habitat attributes to population dynamics. In the future, models

may arise for ungulates that feature individual-animal responses to landscape patterns (Grimm and Railsback 2005, Breckling et al. 2006, Simpson et al. 2009) that can predicate animal choices upon state dependency (Clark and Mangel 2000) to identify emergent population-level properties such as nutritional condition and fitness.

No matter the model type or application, a fundamental issue involves quantifying nutritional resources in ways that are relevant to reproduction and survival if meaningful linkages between habitat and ungulate productivity are to be portrayed. Recognition is increasing that estimates of forage quantity and even quality from standard vegetation surveys may fail as reliable measures of nutritional values of plant communities (Searle et al. 2007, Moore et al. 2010). Herbivores have considerable ability to select plants and plant parts and adjust foraging strategies such that nutrition remains relatively constant despite substantial variation in forage quality and quantity. Searle et al. (2007) coined a term pertaining to these dynamics: foodscapes are the outcome of interactions between forage characteristics and behavioral decisions made by the foraging animal. Instead of describing landscapes in terms of traditional habitat variables such as vegetation composition, vegetation biomass, cover types, and other similar proxy variables that may have little direct meaning for animal performance, it makes more sense to describe landscapes using metrics reflecting behavioral responses to the nutritional environment of the animal. Examples suggested by Searle et al. (2007) included many of the variables that we sampled, such as bite size and rate, rumination time, travel rate, and others that we did not measure, such as time per feeding station, step length, and feeding time per step.

However, dietary quality and forage intake rate are variables that are directly linked to animal performance, so why not focus on measuring the emergent responses that really count? We think the foodscape concept needs to be further developed in several ways. First, emergent variables such as step rate, bite rate, foraging time, and so forth may serve as surrogate measures of nutritional value of plant communities. But they often may not be useful because variation in step rates, bite rate, foraging time, and so forth may be tools that animals use to help maintain relatively high levels of dietary quality and intake rate despite variation in forage quality and quantity. Thus, step rates, for example, might vary in response to varying vegetation, but dietary quality or intake rate may not. Second, measuring many of these foraging behavior variables may be difficult in wild settings, and new technologies may be required to sample many of the animal attributes listed by Searle et al. (2007).

We posit that the gold standard for measuring fine-scale relations between habitat and nutrition is captive, trained animals. Captive ungulates have been used in place of wild herbivores for studies of nutrition and foraging for decades, but they have been underutilized (Hester et al. 2000). There generally are no valid alternatives to using captive animals to measure many of the emergent properties discussed by Searle et al. (2007), or, more broadly, to measure explicit fine-scale relationships among ecological site conditions, succession, vegetative states, and ungulate nutrition (Fig. 1) that are crucial for developing effective habitat management strategies and landscape planning. We do not mean to ignore certain landscape-scale tests of nutrition-

explicit hypotheses (e.g., Bishop et al. 2009, Hurley et al. 2014). But such approaches often may be unsuitable for identifying fine-scale mechanistic relations between habitat and nutritional responses, and would have incompletely satisfied our objective of understanding ecological and successional influences on elk nutrition in our study region.

MANAGEMENT IMPLICATIONS

Habitat Evaluation and Planning

Using ecological principles as a base for landscape planning may provide a basis for integrating nutritional resources into habitat evaluation and planning across landscapes, because central features of landscape ecology and planning include variation in temperature, precipitation, historical and recent disturbance, and plant succession (Landres et al. 1999). For landscape planning on behalf of wildlife, Haufler (1994) called for improvements in accounting for underlying ecological influences and forest succession on resources important for wildlife. He proposed using an ecosystem diversity matrix for planning purposes. Such a matrix is multi-dimensional, with ecological site potentials based on potential natural vegetation categories depicted in 1 dimension, successional stage a second dimension, and various habitat treatments such as wildfire or thinning depicted in additional dimensions. Dimensions in the matrix can be categorical or represented as points along ecological gradients such as succession, soils, landform, climate, and, potentially, climate change. Thus, some of the dimensions could instead be represented with linear or nonlinear functions. We used both for our nutrition model, wherein we depicted key vegetation attributes that related to nutritional value of plant communities along successional gradients within potential natural vegetation categories. Potential applications for management and planning include depiction of spatially explicit distribution of nutritional resources across time, identification of where adequate and inadequate nutritional resources exist, location of where management might be best used to improve these resources, and location of restrictions of human development and activities to protect nutritionally superior areas.

For our study region, landscape planning to include spatially explicit depictions of nutritional resources should 1) reflect ecological context; 2) incorporate influences of disturbance and succession; 3) facilitate research of nutrition's influences on ungulate populations; and 4) readily integrate into management plans of land and wildlife management agencies. Our findings were used to develop a spatially explicit, digital nutritional resource mapping model for wildlands in our study region. Using extant wild-elk telemetry data sets, the nutrition map served to develop a nutrition-explicit resource selection function model suitable for planning by land management agencies in the region (see <http://www.fs.fed.us/pnw/research/elk/index.shtml>). This work provides 1 example of how nutritional data developed at fine scales can be integrated with and evaluated using data collected from wild elk at broad scales (Fig. 1) and packaged for landscape planning and evaluation. Improvements in the approach will likely occur as the science of landscape ecology and planning develops in the future (Leitão and Ahern 2002).

The specific relationships we found probably will not directly apply in other ecological regions, and thus routinely accounting

for nutrition for agency planning and practical habitat management in other areas will require that ecologists provide nutritional information locally. We think the crucial value of tame animals for fine-scale nutritional assessments is clear, but their availability throughout North America remains low, and the increasing concerns about disease and high costs of maintaining them may preclude their use even more. Thus, alternative approaches are needed to quantify nutritional resources at fine scales and describe foodscapes for habitat management and planning. The Hobbs and Swift (1985) and Hanley et al. (2012) approaches for integrating forage quality and quantity offer advantages over earlier strategies and might be improved by expanding the 2-dimensional array of forage quality and quantity to include a third dimension, bite mass, to incorporate the effects of this variable on intake rate (Illius 1997, Shipley 2007) although we recognize that reliable estimates of bite mass probably require the use of tame animals. To effectively use the approach, which plant parts and species that are palatable and relatively nutritious also is important knowledge (Hanley et al. 2012) and is typically unknown in many areas. Finally, using the approach simply as a carrying-capacity algorithm, where units of final output are animal numbers, may underutilize the full potential of the strategy. For example, the approach might be well-suited to consider forage quality and quantity of plant communities across landscapes as a basis to model animal behavior and population dynamics in relation to variation in nutritional resources.

Regarding animal-based, fine-scale approaches, many options potentially exist (Searle et al. 2007), and new options will undoubtedly arise as technology increases. Whatever the approach, it is incumbent upon nutritional ecologists to rigorously confirm that new techniques portray nutritional resources in ways that are relevant and accurate for linking habitat conditions to animal performance. Indiscriminant use of proxy variables (Searle et al. 2007), inaccurate new technologies, and inappropriate applications of estimates from forage quality and quantity surveys (Hobbs and Swift 1985) may do more harm than good for advancing the science of nutritional ecology. At fine scales, captive animals likely provide the best approach in many cases to evaluate accuracy and relevance of new technologies and nutrition-explicit habitat evaluation approaches.

Habitat Management

Our findings indicate that early seral stages are essential for providing good nutrition for elk in the region. The shift in forest management policy on federal lands in the early 1990s set in motion a trend of declining amounts of early seral forests (Swanson et al. 2014) such that representation of these stages on current landscapes is markedly lower than at any time since at least the 1400s (Weisberg and Swanson 2003). Moreover, because federal public lands predominantly occur at higher elevations (including PSS and MHS habitats) more so than do private timberlands, our findings suggest that creation of early seral vegetation has been most reduced in areas with the greatest potential to provide the best nutrition for elk. Thus, the question about effective ways to create such habitat, and how much early seral habitat is needed, has become a central issue (Oregon Department of Fish and Wildlife 2008).

Habitat management to benefit elk will be most effective if integrated in long-term landscape management plans where habitat needs of elk are tied to manipulations for a variety of other purposes. These may include reducing wildfire potential, production of biofuels, alteration of forest density, restoring forest health, and commercial forestry (Sporting Conservation Council, 2008: 38–39). We sampled stands managed by 2 practices commonly used on private and state-owned timberlands in the region, namely clearcut logging with various site-preparatory treatments to support growth of planted conifers, and commercial thinning. Because the stands that we sampled ranged in age up to 650 years old, our data reflect a long history of changing forestry practices and natural disturbance events, from intensive silviculture in recent years to catastrophic wildfires of the past (Weisberg and Swanson 2003). In light of how rapidly plant succession occurs, our study indicates a rapid conversion to dense conifer overstories and understories dominated by shade-tolerant understory species regardless of how the habitats are treated. Hence, where the management goal is to provide landscapes with mosaics of early and advanced seral stages for elk and other wildlife, the effort will have to be continuous.

One implication of our findings is clear from a long-term, regional perspective: the nutritional suitability of landscapes for elk herds depends far more on the extent of active management and natural disturbance regimes across landscapes than whether or not herbicides are used to support early growth of planted conifers. We were unable to directly compare herbicide-treated versus untreated early seral stands, but the forage base was far superior after clearcut logging even 2–3 years after herbicide applications compared to unharvested stands, and was generally superior to that in the commercial thinning operations that we encountered (Jenkins and Starkey 1996). Nevertheless, perceptions are that prescribed burning as an alternate site preparation treatment may provide better nutrition in early seral stages (Washington Department of Fish and Wildlife 2006, Oregon Department of Fish and Wildlife 2008). Vegetation differences resulting from the 2 approaches are unclear. Following clearcutting and prescribed burning, Franklin and Dyrness (1988) identified initial stages in the early seral window in which forage abundance was greatly reduced and plant composition was similar to the plant composition that we documented after herbicide application. They also noted that logging in the absence of broadcast burning only modestly increased shade-intolerant species, many of which are palatable and relatively nutritious for elk.

Silvicultural options that extend the early seral period of forage (AccSpp) abundance would clearly be beneficial for elk. Pre-commercial thinning in stands 10–15 years old and planting seedling conifers at wider spacing may help. However, Alaback and Herman (1988) suggested otherwise, and thus better information is needed to evaluate how such practices might lengthen the early seral window. We caution that more frequent use of herbicides than we encountered (typically a site preparation application followed by a release spray after planting) or important advances in herbicide technology that increase the duration of suppressing effects may obviate the nutrition benefits of logging to elk that we documented. Maintaining a balance between rapidly growing young conifers and providing good

forage for ungulate herds potentially has important public relations benefits.

Our study indicated modest improvement in nutritional value after thinning in stands 20–60 years old, mainly in terms of DE and DP intake rates. Our findings accord with studies of thinning effects on understory vegetation, and together suggest marginal potential for thinning to improve nutritional resources for elk (Alaback and Herman 1988, Jenkins and Starkey 1996, Thomas et al. 1999). However, thinning treatments we evaluated reduced overstory canopy cover modestly (to as low as 68% cover at the time we sampled them), and greater overstory removal may provide greater nutritional benefits. Thinning also strongly increased the abundance of less palatable species, so site treatments after thinning that reduce the abundance of evergreen shrubs and ferns may increase the nutritional benefits of thinning. Finally, we did not evaluate thinning effects in the higher-elevation, wetter habitats (PSS and MHS). But in light of the reduced dominance of unpalatable, lower-quality plant species, and longer persistence of higher-quality early seral vegetation after disturbance, we would expect that thinning in these types may provide substantially greater nutritional benefit than in the lower elevation WHS habitats. More work is needed to clarify these issues.

Our nutrition prediction equations (Tables 11 and 12) provide a basis to evaluate nutritional value of habitat for local applications or for types of habitat within our study region or various habitat treatments that we were unable to specifically evaluate. These equations are most appropriate for estimating changes in nutritional value of plant communities after habitat treatments, for example, that stem principally from changes in plant species composition and abundance. They should not be used for evaluating habitat treatments designed to change plant chemistry and forage quality, such as fertilization, or for evaluating nutritional value of planted, non-native pastures and food plots. The equations are applicable for stand-level evaluations, ≥ 0.5 ha, in reasonably homogenous stands. For the 2 DDE_{All} equations for WHS (Table 11), we consider the separate handling of NeuSpp and SelSpp in the multiple regression equation to be of greater biological value with perhaps greater management utility than the simpler exponential equation that included only AccSpp. However, the multiple regression equation may provide unrealistically low estimates of dietary DE in habitats that have higher levels of NeuSpp and SelSpp than were used to develop the equation. This consequence would be due to the negative influence on DDE of the quadratic term in the equation, an issue revealed based on an independent analysis in Washington (E. H. Merrill, University of Alberta, personal communication). For those stands where AccSpp is higher than what we encountered ($\geq 1,500$ kg/ha; Fig. 56A,B), the exponential equation should be used. We have the same concern for the exponential versus the multiple regression dietary DE equations for PSS and MHS (Table 11): if AccSpp is $\geq 1,000$ kg/ha in these forest series (Fig. 56C), then the exponential equation is superior.

Finally, our selection ratings (Appendix E) for plant species that were relatively rare ($n < 10$ pens) should be viewed with some caution. Small, rare plant species were likely to be reported as avoided simply because elk rarely encountered them during the trials, not necessarily because elk found them to be unpalatable.

Additionally, and perhaps of more concern, plants that were in few pens tended to be categorized as neutral simply because of the small sample size (i.e., probability that the Ivlev index = 0 increased as n declined). Those species that were locally abundant in the few pens that they occurred and from which elk occasionally took a few bites but nevertheless seemed to avoid had a high probability of being rated as neutral species when they were probably avoided. We consider bristly manzanita (*Arctostaphylos columbiana*), chinquapin (*Castanopsis chrysophylla*), Scot's broom (*Cytisus scoparius*), western dock (*Rumex occidentalis*), and Indian basket grass (*Xerophyllum tenax*) to be primary examples of this (Appendix E).

Our results provide little specific guidance for questions involving broad-scale applications. For example, how much area across an elk summer range should be retained in early-seral habitats to support or increase elk, and how might the juxtaposition of nutritional resources and other habitat attributes such as roads and cover influence population responses to current and future habitat conditions? Providing adequate habitat particularly for rare species such as spotted owls (*Strix occidentalis*) and other conservation programs that favor late-seral forest stages has and will continue to limit areas available for elk habitat management, placing an even greater premium on judicious management of habitat on behalf of elk where it is permitted. Further, elk are widely dispersed in summer, suggesting an extensive approach is needed where nutritionally superior habitat types also are widely spread across summer ranges. Thus, the question of how much of nutritionally superior habitat should be created is crucial. Answering the question will require modeling efforts beyond our work presented herein, perhaps using nutrition-based carrying-capacity models for elk such as that developed for black tailed deer (Hanley et al. 2012), nutrition-explicit resource selection models, or even various types of simulation models (e.g., Moen et al. 1997).

SUMMARY

- We used captive, trained female elk and their calves held in pens to measure the nutritional value of plant communities across succession and ecological gradients at 3 study areas in western Washington and Oregon. We measured overstory and understory plant community characteristics available to elk and related these characteristics to foraging responses.
- In early seral stages following stand-replacing disturbance, shade-intolerant plant species quickly established, resulting in diverse and productive understory plant communities of 2,000–4,000 kg/ha that lasted 10–15 years in lower-elevation forest zones and 15–40 years in higher-elevation forest zones. Thereafter, overstory canopies generally closed rapidly, shade-tolerant species reestablished dominance in the understory, understory production declined to 100–1,000 kg/ha, and these levels of production held through late seral stages.
- Digestible energy content was higher in many shade-intolerant plant species, and thus community-wide DE levels in forage declined as vegetation shifted from shade-intolerant to shade-tolerant species as succession advanced. Forage that satisfied nutritional requirements of lactating elk was abundant only in early successional stages.

- Elk primarily selected for palatable, shade-intolerant species but shifted diets to include more lower-quality, shade-tolerant species as abundance of the more palatable species declined to low levels. Thus, dietary DE levels declined with advancing succession. In low to moderate elevation forest zones, dietary DE levels were highest and approached requirement for lactating females in early successional stages but were substantially below requirements in closed-canopy forests. This pattern held for higher-elevation areas supporting PSS and MHS forests, although dietary DE more frequently exceeded requirements in early seral stages, and the magnitude of deficiency was less in closed-canopy forests. Hence, ecological site conditions and succession had strong influences on dietary DE. We found differences in dietary DE between study areas, but most of these differences were largely attributable to differences in the amount of each habitat type at the study areas.
- Dietary DP exhibited only weak trends with succession. Instead, DP was greater on sites with higher soil moisture and perhaps soil nitrogen, tended to be higher under forest canopies, and was lowest in the drier forest habitats of our study.
- Intake rates of DE followed a similar pattern observed for dietary DE levels, with higher levels of DE intake occurring in early seral stages and markedly deficient intake rates of DE in closed-canopy forests. Intake rate of protein was largely invariant to successional stage, was lowest in the drier low-elevation habitats, and, on average, generally satisfied requirements except in these lower-elevation habitats.
- Rate of body fat loss in adult lactating females significantly accelerated when abundance of the palatable, shade-intolerant species was low, reflecting patterns of dietary DE and intake rates of DE. Growth of calves was related to nutrition of their mothers, although we found only weak relations between abundance of palatable, shade-intolerant species and calf growth. Rates of body fat change and calf growth indicated poor overall nutrition that limited performance well below levels that elk are capable.
- We developed equations to predict dietary DE and DP levels and intake rates of both based primarily on composition and abundance of palatable species and indicator species of relatively moist soils. These equations illustrated nutrition-succession trajectories for the major habitat types of our study areas, which in turn demonstrated influences of plant succession and ecological gradients on nutritional value of plant communities.
- Our results demonstrated that nutritional resources, measured in units that are relevant to reproductive performance of elk, are a predictable function of disturbance, succession, and ecological gradients and thus have substantial value for management and planning purposes.
- Overall, our data identified the predominance of habitats that provide strongly inadequate levels of nutrition for lactating elk and their calves on summer ranges of our study areas, identified the essential role of early seral stages for satisfying nutritional needs of these animals, and thus identified the need for appropriate habitat management.
- Habitat management programs in areas where reasonably productive elk herds are desired will have to be extensive in

scope, maintained in perpetuity primarily on summer range because of the rapid rate of plant succession, and will generally have to be linked to vegetation management and resource use designed for other objectives. Thus, providing adequate elk nutrition will require careful integration of nutritional ecology with landscape planning in the forests of the Pacific Northwest.

ACKNOWLEDGMENTS

Rocky Mountain Elk Foundation very generously supported this study. Also, in alphabetical order: American Forest Resource Council, Boise Cascade Corporation, Bureau of Land Management, Crown Pacific, Hampton Tree Farms, Muckleshoot Indian Tribe, National Council for Air and Stream Improvement, Oregon Department of Fish and Wildlife, Oregon Forest Industries Council, Plum Creek Timber Company, Portland Chapter of Safari Club International, Rayonier Timberlands, Swinomish Indian Tribal Community, U.S. Department of Health and Human Services Administration for Native Americans Environmental Regulatory and Enhancement Grant, U.S. Fish and Wildlife Service Tribal Wildlife Grant, U.S. Forest Service Pacific Northwest Research Station, Washington Department of Fish and Wildlife, Washington Department of Natural Resources, Washington Forest Protection Association, Weyerhaeuser Company, and Willamette Industries. We also wish to thank T. Toman, B. Richardson, D. Wiley, and B. Bastion of Rocky Mountain Elk Foundation; B. Anderson (retired), E. Arnett, R. Heninger, and T. Melchior of the Weyerhaeuser Company; L. Hicks of Plum Creek Timber; D. Varland of Rayonier Timberlands; T. Garren, K. Phelps, D. Rock, and S. Rock of the National Council for Air and Stream Improvement; A. Stringer and K. Cattoms of the Campbell Group; D. Irish and B. Castillo of Oregon Department of Fish and Wildlife; D. Bernard and G. Netzer of Safari Club; B. Alverts (retired), T. Johnson, and G. Buckner (now with Oregon Department of Fish and Wildlife) of the Bureau of Land Management; M. Davison, L. Bender, and J. Nelson of Washington Department of Fish and Wildlife; D. Vales, M. Middleton, M. Calvert, and the Wildlife Committee of the Muckleshoot Indian Tribe; J. W. Thomas of the Boone and Crockett Club; L. Thompson of Crown Pacific; T. Wilbur of Swinomish Tribal Community; D. Gay of the Mt. Baker-Snoqualmie National Forest; R. Warner of the University of Illinois at Urbana-Champaign; and the many field technicians who helped sample and weigh vegetation, monitor elk, and build fences. We also thank I. Lama of National Council of Air and Stream Improvement and L. Veilleux, Environmental Consultant, for providing the Spanish and French translations of the abstract. Reviews by D. Hewitt and E. Merrill greatly helped to improve the manuscript.

LITERATURE CITED

- Alaback, P. B. 1982. Dynamics of understory biomass in sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932-1948.
- Alaback, P. B., and F. R. Herman. 1988. Long-term response of understory vegetation to stand density in *Picea-Tsuga* forests. *Canadian Journal of Forest Research* 18:1522-1530.
- Allden, W. G., and I. A. M. Whittaker. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* 21:755-766.

- Allredge, M. W., J. M. Peek, and W. A. Wall. 2002. Nutritional quality of forages used by elk in northern Idaho. *Journal of Range Management* 55:253–259.
- Arnold, G. W. 1985. Regulation of forage intake. Pages 81–102 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Austin, D. D., P. J. Urness, and L. C. Fierri. 1983. Spring livestock grazing affects crested wheatgrass regrowth and winter use by mule deer. *Journal of Range Management* 36:589–593.
- Babin, J. S., D. Fortin, J. F. Wilmshurst, and M.-E. Fortin. 2011. Energy gains predict the distribution of plains bison across populations and ecosystems. *Ecology* 92:240–252.
- Bailey, D. W., J. F. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management* 49:386–400.
- Beck, J. L., and J. M. Peek. 2005. Great Basin summer range forage quality: do plant nutrients meet elk requirements? *Western North American Naturalist* 65:516–527.
- Bender, L. C., M. A. Davison, J. G. Cook, R. C. Cook, and P. B. Hall. 2006. Assessing elk population status and potential performance in the Nooksack area, Washington. *Northwestern Naturalist* 97:98–106.
- Bergerud, A. T., and L. Russell. 1964. Evaluation of rumen food analysis for Newfoundland caribou. *Journal of Wildlife Management* 28:809–814.
- Bergman, C. M., J. M. Fryxell, and C. C. Gates. 2000. The effect of tissue complexity and sward height on the functional response of wood bison. *Functional Ecology* 14:61–69.
- Berryman, A. A., M. L. Arce, and B. A. Hawkins. 2002. Population regulation, emergent properties, and a requiem for density dependence. *Oikos* 99:600–606.
- Bishop, C. J., G. C. White, D. J. Freddy B. E. Watkins, and T. R. Stephenson. 2009. Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs* 172:1–28.
- Blair, R. M., R. Alcaniz, and A. Harrell. 1983. Shade intensity influences the nutrient quality and digestibility of southern deer browse leaves. *Journal of Range Management* 36:257–264.
- Bomar, L. K. 2000. Broad-scale patterns of elk recruitment in Idaho: relationships with habitat quality and effects of data aggregation. Thesis, University of Idaho, Moscow, USA.
- Boonstra, R. 2013. Reality as the leading cause of stress: rethinking the impact of chronic stress in nature. *Functional Ecology* 27:11–23.
- Bormann, B. T., and D. S. DeBell. 1981. Nitrogen content and other soil properties related to age of red alder stands. *Journal of the Soil Science Society of America* 45:428–432.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281–300.
- Breckling, B., U. Middelhoff, and H. Reuter. 2006. Individual-based models as tools for ecological theory and application: understanding the emergence of organizational properties in ecological systems. *Ecological Modelling* 194:102–113.
- Bunnell, F. L., and D. J. Vales. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. *Canadian Journal of Forestry Research* 20:1001–1007.
- Canon, S. K., P. J. Urness, and N. V. DeByle. 1987. Foraging behavior and dietary nutrition of elk in burned aspen forest. *Journal of Range Management* 40:433–438.
- Carpenter, L. H. 1998. Deer in the West. Pages 1–10 in J. C. DeVos, Jr., editor. *Proceedings of the 1997 deer/elk workshop*. Arizona Game and Fish Department, Rio Rico, Arizona, USA.
- Caughley, G. 1979. What is this thing called carrying capacity? Pages 2–8 in M. S. Boyce and L. D. Hayden-Wing, editors. *North American elk: ecology, behavior, and management*. University of Wyoming, Laramie, USA.
- Chacon, E., and T. H. Stobbs. 1976. Influence of progressive defoliation of a grass sward and the eating behavior of cattle. *Australian Journal of Agricultural Research* 27:709–727.
- Christensen, A. G., L. J. Lyon, and J. W. Unsworth. 1993. Elk management in the Northern Region: considerations in forest plan updates or revisions. U.S. Department of Agriculture, Forest Service, General Technical Report INT-303, Ogden, Utah, USA.
- Clark, C. E., and M. Mangel. 2000. *Dynamic state variables models in ecology*. Oxford University Press, New York, New York, USA.
- Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646–663.
- Cook, J. G. 2002. Nutrition and food. Pages 259–349 in E. D. Toweill and J. W. Thomas, editors. *North American elk: ecology and management*. Smithsonian Institution Press, Washington, D.C., USA.
- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs* 155:1–61.
- Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during late summer and fall. *Journal of Wildlife Management* 60:528–541.
- Cook, J. G., T. W. Stutzman, C. W. Bowers, K. A. Brenner, and L. L. Irwin. 1995. Spherical densimeters produce biased estimates of forest canopy cover. *Wildlife Society Bulletin* 23:711–717.
- Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. *Journal of Wildlife Management* 65:973–987.
- Cook, R. C., J. G. Cook, T. R. Stephenson, W. L. Myers, S. M. McCorquodale, D. J. Vales, L. L. Irwin, P. B. Hall, R. D. Spencer, S. L. Murphie, K. A. Schoenecker, and P. J. Miller. 2010. Revisions of rump fat and body scoring indices for deer, elk, and moose. *Journal of Wildlife Management* 74:880–896.
- Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Schoenecker, F. Geyer, P. B. Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J. Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. *Wildlife Monographs* 184:1–45.
- Coughenour, M. B., and R. J. Singer. 1996. Yellowstone elk population responses to fire—a comparison of landscape carrying capacity and spatial-dynamic ecosystem modeling approaches. *Proceedings of the Biennial Conference on the Greater Yellowstone Ecosystem* 2:169–179.
- Creel, S., D. Christianson, S. Lily, and J. A. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315:960.
- Creel, S., D. A. Christianson, and J. A. Winnie, Jr. 2011. A survey of the effects of wolf predation risk on pregnancy rates and calf recruitment in elk. *Ecological Applications* 21:2847–2853.
- Creel, S., J. Winnie Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397.
- Crête, M., and R. Courtois. 1997. Limiting factors might obscure population regulation of moose (*Cervidae: Alces alces*) in unproductive boreal forests. *Journal of Zoology, London* 242:765–781.
- Crête, M., and J. Huot. 1993. Regulation of a large herd of migratory caribou: summer nutrition affects calf growth and body reserves of dams. *Canadian Journal of Zoology* 71:2291–2296.
- Dale, B. W., L. G. Adams, W. B. Collins, K. Joly, P. Valkenburg, and R. Tobey. 2008. Stochastic and compensatory effects limit persistence of variation in body mass of young caribou. *Journal of Mammalogy* 89:1130–1135.
- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33:140–158.
- Davidson, G. A., B. K. Johnson, J. H. Noyes, B. L. Dick, and M. J. Wisdom. 2012. Effect of archer density on elk pregnancy rates and conception dates. *Journal of Wildlife Management* 76:1676–1685.
- Davison, M. A. 2002. Washington State elk herd plan: North Cascade (Nooksack) elk herd. Washington Department of Fish and Wildlife, Olympia, USA.
- de Vries, M. F. W., and C. Daleboudt. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* 100:98–106.
- DeYoung, C. A., D. L. Drawe, T. E. Fulbright, D. G. Hewitt, S. W. Stedman, D. R. Synatzske, and J. G. Teer. 2008. Density dependence in deer populations: relevance for management in variable environments. Pages 203–222 in T. E. Fulbright and D. G. Hewitt, editors. *Wildlife science: linking ecological theory and management applications*. CRC Press, Baton Rouge, Louisiana, USA.
- Drescher, M., I. M. A. Heitkönig, J. G. Raats, and H. H. T. Prins. 2006. The role of grass stems as structural foraging deterrents and their effects on the foraging behavior of cattle. *Applied Animal Behavioral Science* 101:10–26.
- Edge, W. D., S. L. Olson-Edge, and L. L. Irwin. 1990. Planning for wildlife in national forests: elk and mule deer habitats as an example. *Wildlife Society Bulletin* 18:87–98.
- Einarsen, A. S. 1946. Management of black-tailed deer. *Journal of Wildlife Management* 10:54–59.
- Farnsworth, K. D., and J. A. Beecham. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. *American Naturalist* 153:509–526.

- Ferry, M. L., T. S. Peterson, and J. C. Calhoun. 2001. Status of elk populations on the Olympic Peninsula. Olympic Natural Resources Center Conference Proceedings, University of Washington, Olympic Natural Resources Center, Forks, USA.
- Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Canadian Journal of Zoology* 89:419–434.
- Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Pages 401–441 in H. C. Genoways, editor. *Current mammalogy*. Plenum Press, New York, New York, USA.
- Franklin, J. F., and C. T. Dyrness. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, USA.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* 138:478–498.
- Geary, A. B. 2014. Succession, herbicides, forage nutrition and elk body condition at Mount St. Helens, Washington. Thesis, University of Alberta, Edmonton, Canada.
- Gerhart, K. L., D. E. Russell, D. Van DeWetering, R. G. White, and R. D. Cameron. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence of lactational infertility. *Journal of Zoology*, London 242:17–30.
- Gill, R. M. A., A. L. Johnson, A. Francis, K. Hiscocks, and A. J. Peace. 1996. Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. *Forest Ecology and Management* 88:31–46.
- Gillingham, M. P., K. L. Parker, and T. A. Hanley. 1997. Forage intake by black-tailed deer in a natural environment: bout dynamics. *Canadian Journal of Zoology* 75:1118–1128.
- Goering, H. K., and P. J. Van Soest. 1970. Forage analyses (apparatus, reagents, procedures, and some applications). United States Department of Agriculture, Agriculture Handbook 379, Washington, D.C., USA.
- Grey, P. B., and F. A. Servello. 1995. Energy intake relationships for white-tailed deer on winter browse diets. *Journal of Wildlife Management* 59:147–152.
- Grimm, V., and S. F. Railsback. 2005. *Individual-based modeling and ecology*. Princeton University Press, Princeton, New Jersey, USA.
- Haigh, J. C., and R. J. Hudson. 1993. *Farming wapiti and red deer*. Mosby-Year Book, St. Louis, Missouri, USA.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos* 79:209–218.
- Hanley, T. A., R. G. Cates, B. Van Horne, and J. D. McKendrick. 1987. Forest stand age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. Pages 9–17 in F. D. Provenza, J. T. Flinders, and E. D. McArthur, compilers. *Proceedings Symposium on plant-herbivore interactions*. U.S. Department of Agriculture, Forest Service, General Technical Report INT-222, Washington, D.C., USA.
- Hanley, T. A., D. E. Spalinger, K. J. Mock, O. L. Weaver, and G. M. Harris. 2012. Forage resource evaluation system for habitat—deer: an interactive deer habitat model. U.S. Department of Agriculture, Forest Service, General Technical Report, PNW-GTR-858, Washington, D.C., USA.
- Happe, P. J., K. J. Jenkins, E. E. Starkey, and S. H. Sharrow. 1990. Nutritional quality and tannin astringency of browse in clearcut and old-growth forests. *Journal of Wildlife Management* 54:557–566.
- Harder, J. D., and R. L. Kirkpatrick. 1994. *Physiological methods in wildlife research*. Pages 275–306 in T. A. Bookhout, editor. *Research and Management techniques for wildlife and habitats*. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Harper, J. A. 1987. *Ecology and management of Roosevelt elk in Oregon*. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.
- Haufler, J. B. 1994. An ecological framework for forest planning for forest health. *Journal of Sustainable Forestry* 2:307–316.
- Hebblewhite, M., E. Merrill, and G. McDermid. 2008. A multi scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs* 78:141–161.
- Henderson, J. A., R. D. Leshner, D. H. Peter, and D. C. Shaw. 1992. *Field guide to the forested plant associations of the Mt. Baker-Snoqualmie National Forest*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. R6-ECOL-TP-001-91, Washington, D.C., USA.
- Hester, A. J., L. Edenius, R. M. Buttenschon, and A. T. Kuiters. 2000. Interactions between forests and herbivores: the role of controlled grazing experiments. *Forestry* 73:381–391.
- Hett, J., R. Taber, J. Long, and J. Schoen. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabilis* forest, western Washington. *Environmental Management* 2:561–566.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. An illustrated manual. University of Washington Press, Seattle, USA.
- Hjeljord, O., and T. Histol. 1999. Range-body mass interactions of a northern ungulate—a test of hypothesis. *Oecologia* 119:326–339.
- Hobbs, N. T. 2003. Challenges and opportunities in integrating ecological knowledge across scales. *Forest Ecology and Management* 18:223–238.
- Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy and nitrogen-based estimates of elk winter-range carrying capacity. *Journal of Wildlife Management* 46:12–21.
- Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49:814–822.
- Holter, J. B., and H. H. Hayes. 1977. Growth in white-tailed deer fawns fed varying energy and constant protein. *Journal of Wildlife Management* 41:506–510.
- Houston, D. B. 1982. *The northern Yellowstone elk: ecology and management*. Macmillan Publishing Company, New York, New York, USA.
- Hudson, R. J., and J. Z. Adamczewski. 1990. Effect of supplementing summer ranges on lactation and growth of wapiti (*Cervus elaphus*). *Canadian Journal of Animal Science* 70:551–560.
- Hudson, R. J., and R. J. Christopherson. 1985. Maintenance metabolism. Pages 121–143 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Hudson, R., and J. C. Haigh. 2002. Physical and physiological adaptations. Pages 199–258 in D. E. Toweill and J. W. Thomas, editors. *North American elk: ecology and management*. Smithsonian Institution Press, Washington, D.C., USA.
- Hudson, R. J., and M. T. Niefeld. 1985. Effect of forage depletion on the feeding rate of wapiti. *Journal of Range Management* 38:80–82.
- Hudson, R. J., and W. G. Watkins. 1986. Foraging rates of wapiti on green and cured pastures. *Canadian Journal of Zoology* 64:1705–1708.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Hurley, M. A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K. A. Taylor, W. K. Smith, P. Zager, and C. Bonenfant. 2014. Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philosophical Transactions of the Royal Society B* 369:1–15.
- Hutchins, N. R. 2006. *Diet, nutrition, and reproductive success of Roosevelt elk in managed forests of the Olympic Peninsula, Washington*. Thesis, Humboldt State University, Arcata, California, USA.
- Illius, A. W. 1997. Advances and retreats in specifying the constraints on intake in grazing ruminants. *Proceedings of the International Grasslands Congress* 18:39–44.
- Illius, A. W., and I. J. Gordon. 1999. Scaling up from functional response to numerical response in vertebrate herbivores. Pages 397–497 in H. Olff, V. K., Brown, and R. H. Drent, editors. *Herbivores: between predators and plants*. Blackwell Science, Oxford, United Kingdom.
- Irwin, L. L., and J. M. Peek. 1983. Elk, *Cervus elaphus*, foraging related to forest management and succession in Idaho. *Canadian Field-Naturalist* 97:443–447.
- Jenkins, K., and E. Starkey. 1996. Simulating secondary succession on elk forage values in a managed forest landscape, western Washington. *Environmental* 20:715–724.
- Jiang, A., and R. J. Hudson. 1992. Estimating forage intake and energy requirement of free-ranging wapiti (*Cervus elaphus*). *Canadian Journal of Zoology* 70:675–679.
- Johnson, B. K., M. J. Wisdom, and J. G. Cook. 2005. Issues of elk productivity for research and management. Pages 81–93 in M. J. Wisdom, editor. *The Starkey Project: a synthesis of long-term studies of elk and mule deer*. Alliance Communications Group, Lawrence, Kansas, USA.
- Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 64:450–462.
- Krebs, C. J. 2002. Beyond population regulation and limitation. *Wildlife Research* 29:1–10.
- Kuttel, M. P. 1975. Second report on the Willapa Hills elk herd, Sept. 1, 1974–April 1, 1975. Washington Game Department, Olympia, USA.
- Landres, P. B., P. Morgan, and R. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* 9:1179–1188.

- Launchbaugh, K. L., F. D. Provenza, and J. A. Pfister. 2001. Herbivore response to anti-quality factors in forage. *Journal of Range Management* 54:431–440.
- Lautenschlager, R. A., and T. P. Sullivan. 2002. Effects of herbicide treatments on biotic components in regenerating northern forests. *Forestry Chronicle* 78:695–731.
- Leege, T. A. 1984. Guidelines for evaluating and managing summer elk habitat in northern Idaho. Bulletin 11, Idaho Department of Fish and Wildlife, Boise, Idaho, USA.
- Leitão, A. B., and J. Ahern. 2002. Applying landscape ecological concepts and metrics in sustainable landscape planning. *Landscape and Urban Planning* 59:65–93.
- Leslie, Jr., D. M., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests in western Washington. *Journal of Wildlife Management* 48:762–775.
- Lopez, E. 2006. Natural selenium and planted forages: effects on mule deer and elk in Washington. Dissertation, Washington State University, Pullman, USA.
- Lyon, L. J., T. N. Lonner, J. P. Weigand, C. L. Marcum, W. D. Edge, J. D. Jones, D. W. McCleerey, and L. L. Hicks. 1985. Coordinating elk and timber management. Final Report of the Montana Cooperative Elk-Logging Study 1970–1985. Montana Department of Fish, Wildlife and Parks, Bozeman, USA.
- MacCracken, J., and R. Hansen. 1984. Seasonal foods of blacktailed jackrabbits and Nuttall cottontails in southeastern Idaho. *Journal of Range Management* 37:256–259.
- Mackie, R. J., K. L. Hamlin, D. F. Pac, G. L. Dusek, and A. K. Wood. 1990. Compensation in free-ranging deer populations. *Transactions of the North American Wildlife and Natural Resource Conference* 55:518–526.
- Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals. Chapman and Hall, New York, New York, USA.
- Manly, B., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Ericson. 2002. Resource selection by animals – statistical design and analysis of field studies. Second edition. Kluwer Academic Publishers, London, England.
- Martin, J. S., and M. M. Martin. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins, and protein-precipitation constituents in mature foliage of six oak species. *Oecologia (Berlin)* 54:205–211.
- Mautz, W. W., J. Kanter, and P. J. Pekins. 1992. Seasonal metabolic rhythms of captive female white-tailed deer: a reexamination. *Journal of Wildlife Management* 56:656–661.
- McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. *Ecology* 90:1400–1411.
- McArthur, C., P. B. Banks, R. Boonstra, and J. S. Forbey. 2014. The dilemma of foraging herbivores: dealing with food and fear. *Oecologia* 176:677–689.
- McArthur, C., C. T. Robbins, A. E. Hagerman, and T. A. Hanley. 1993. Diet selection by a ruminant generalist browser in relation to plant chemistry. *Canadian Journal of Zoology* 71:2236–2243.
- McCorquodale, S. M., S. M. Knapp, M. A. Davison, J. S. Bohannon, C. D. Danilson, and W. C. Madsen. 2012. Mark-resight and sightability modeling of a western Washington elk population. *Journal of Wildlife Management* 77:359–371.
- McCullough, D. R. 1984. Lessons from the George Reserve, Michigan. Pages 211–242 in L. K. Halls, editor. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- McCullough, D. R. 1999. Density dependence and life history strategies of ungulates. *Journal of Mammalogy* 80:1132–1146.
- Merrill, E. H. 1987. The population dynamics and habitat ecology of elk in the Mount St. Helens blast zone. Dissertation, University of Washington, Seattle, USA.
- Merrill, E. H. 1994. Summer foraging ecology of wapiti (*Cervus elaphus roosevelti*) in the Mount St. Helens blast zone. *Canadian Journal of Zoology* 72:303–311.
- Merrill, E. H., A. Callahan-Olson, K. J. Raedeke, and R. D. Tabler. 1995. Elk (*Cervus elaphus roosevelti*) dietary composition and quality in the Mount St. Helens blast zone. *Northwest Science* 69:9–18.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013a. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology* 94:1245–1256.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeko, H. Sawyer, and P. J. White. 2013b. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16:1023–1030.
- Minson, D. J. 1990. Forage in ruminant nutrition. Academic Press, New York, New York, USA.
- Minson, D. J., and J. R. Wilson. 1994. Prediction of intake as an element of forage quality. Pages 533–563 in G. C. Fahey, editor. *Forage quality, evaluation, and utilization*. American Society of Agronomy, Madison, Wisconsin, USA.
- Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. *Ecology* 78:505–521.
- Monteith, K. L., R. W. Klaver, K. R. Hersey, A. A. Holland, T. P. Thomas, and M. J. Kauffman. 2015. Effects of climate and plant phenology on recruitment of moose at the southern extent of their range. *Oecologia* 178:1137–1148.
- Moore, B. D., E. R. Lawler, I. R. Wallis, C. M. Beale, and W. J. Foley. 2010. Palatability mapping: a koala's eye view of spatial variation in habitat quality. *Ecology* 91:3165–3176.
- Morales, J. M., D. Fortin, J. L. Frair, and E. H. Merrill. 2005. Adaptive models for large herbivore movements in heterogeneous landscapes. *Landscape Ecology* 20:301–316.
- Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* 166:1–30.
- National Research Council. 1984. Nutrient requirements of beef cattle. Sixth edition. National Academy Press, Washington, D.C., USA.
- National Research Council. 1985. Nutrient requirements of sheep. Sixth revised edition. National Academy Press, Washington, D.C., USA.
- Naylor, L. J., and J. G. Kie. 2004. Monitoring activity of Rocky Mountain elk using recording accelerometers. *Wildlife Society Bulletin* 32:1108–1113.
- Nelson, J. R., and T. A. Leege. 1982. Nutritional requirements and food habits. Pages 323–367 in J. W. Thomas and D. E. Towell, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215–238 in R. J. Hudson and R. G. White, editors. *Bioenergetics of wild herbivores*. CRC Press, Boca Raton, Florida, USA.
- Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. Update edition. John Wiley & Sons, New York, New York, USA.
- Olsen-Rutz, K. M., and P. J. Urness. 1987. Comparability of foraging behavior and diet selection of tractable and wild mule deer. Utah Department of Natural Resources, Publication No. 88-3, Salt Lake City, USA.
- Oosting, H. S. 1956. The study of plant communities. W. H. Freeman and Company, San Francisco, California, USA.
- Oregon Department of Fish and Wildlife. 2008. Oregon black-tailed deer management plan. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.
- Parker, K. L., P. S. Barboza, and M. P. Gillingham. 2009. Nutrition integrates environmental responses to ungulates. *Functional Ecology* 23:57–69.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. *Wildlife Monographs* 143:3–38.
- Peek, J. M., B. Dennis, and T. Hershey. 2002. Predicting population trend of mule deer in south-central Oregon. *Journal of Wildlife Management* 66:729–736.
- Peek, J. M., J. J. Korol, D. Gay, and T. Hershey. 2001. Overstory-understory biomass changes over a 35-year period in southcentral Oregon. *Forest Ecology and Management* 150:267–277.
- Pengelly, W. L. 1963. Timberlands and deer in the northern Rockies. *Journal of Forestry* 61:737–741.
- Penning, P. D., A. J. Parsons, R. J. Orr, and T. T. Treacher. 1991. Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass and Forage Science* 46:15–28.
- Pojar, J., and A. MacKinnon, compilers. 1994. Plants of the Pacific Northwest coast. Lone Pine Publishing, Vancouver, British Columbia, Canada.
- Renecker, L. A., and R. J. Hudson. 1985. Estimation of dry matter intake of free-ranging moose. *Journal of Wildlife Management* 49:785–792.
- Riggs, R. A., S. C. Bunting, and S. E. Daniels. 1996. Prescribed fire. Pages 295–319 in P. R. Krausman, editor. *Rangeland wildlife*. Society for Range Management, Denver, Colorado, USA.
- Riggs, R. A., A. R. Tiedemann, J. G. Cook, T. M. Ballard, P. J. Edgerton, M. Vavra, W. C. Krueger, F. C. Hall, L. D. Bryant, L. L. Irwin, and T. DelCurto. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains ecological province. USDA Forest Service, Research Paper, PNW-RP-527, Pacific Northwest Research Station, Portland, Oregon, USA.
- Riggs, R. A., P. J. Urness, and K. A. Gonzalez. 1990. Effects of domestic goats on deer wintering in Utah oakbrush. *Journal of Range Management* 43:229–234.

- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York, New York, USA.
- Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. J. Baker, C. C. Schwartz, and W. W. Mautz. 1987a. Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology* 68:98–107.
- Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987b. Role of tannins in defending plants against ruminants: Reduction in dry matter digestion? *Ecology* 68:1606–1615.
- Robbins, C. T., R. S. Podbielancik-Norman, D. L. Wilson, and E. D. Mould. 1981. Growth and nutrient consumption of elk calves compared to other ungulate species. *Journal of Wildlife Management* 45:172–186.
- Roloff, G. J., J. J. Millsaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for Rocky Mountain elk. *Journal of Wildlife Management* 65:899–914.
- SAS Institute. 1988. SAS/STAT user's guide. Release 6.03. SAS Institute, Cary, North Carolina, USA.
- SAS Institute. 1993. Introduction to the MIXED procedure. SAS Institute, Cary, North Carolina, USA.
- Schmitt, R. J., and S. J. Holbrook. 2007. The scale and cause of spatial heterogeneity in strength of temporal density dependence. *Ecology* 88:1241–1249.
- Searle, K. R., N. T. Hobbs, and I. J. Gordon. 2007. It's the "foodscape", not the landscape: using foraging behavior to make functional assessments of landscape condition. *Israel Journal of Ecology and Evolution* 53:297–316.
- Shea, S. M., T. A. Breault, and M. L. Richardson. 1992. Herd density and physical condition of white-tailed deer in Florida flatwoods. *Journal of Wildlife Management* 56:262–267.
- Shea, S. M., and J. S. Osborne. 1995. Poor-quality habitats. Pages 193–209 in K. V. Miller and R. L. Marchinton, editors. *Quality whitetails: the why and how of quality deer management*. Stackpole Books, Mechanicsburg, Pennsylvania, USA.
- Shipley, L. A. 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos* 116:1964–1974.
- Sibbald, A. M., P. D. Fenn, W. G. Kerr, and A. S. I. Loudon. 1993. The influence of birth date on the development of seasonal cycles in red deer hinds (*Cervus elaphus*). *Journal of Zoology* 230:593–607.
- Silver, H., N. F. Colovos, J. B. Holter, and H. H. Hayes. 1969. Fasting metabolism of white-tailed deer. *Journal of Wildlife Management* 33:490–498.
- Simpson, S. J., D. Raubenheimer, M. A. Charleston, and F. J. Clissold. 2009. Modelling nutritional interactions: from individuals to communities. *Trends in Ecology and Evolution* 25:53–60.
- Skogland, T. 1986. Density dependent food limitation and maximal production in wild reindeer herds. *Journal of Wildlife Management* 50:314–319.
- Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd; maternal vs. offspring effects. *Oecologia* 84:442–450.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations? *Oikos* 61:401–411.
- Smith, J. L. 1980. Reproductive rates, age structure, and management of Roosevelt elk in Washington's Olympic Mountains. Pages 67–111 in W. MacGregor, editor. *Proceedings of the Western States and Provinces Elk Workshop*, Cranbrook, British Columbia, Canada.
- Spalinger, D. E., S. M. Cooper, D. Martin, and L. A. Shipley. 1997. Is social learning an important influence on foraging behavior in white-tailed deer? *Journal of Wildlife Management* 61:611–621.
- Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* 140:325–321.
- Spalinger, D. E., C. T. Robbins, and T. A. Hanley. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. *Canadian Journal of Zoology* 64:312–321.
- Sporting Conservation Council. 2008. Strengthening America's hunting heritage and wildlife conservation in the 21st century: challenges and opportunities. J. Nobile and M. D. Duda, editors. White House Conference on North American Wildlife Policy. Oct 1–3, 2008, Washington, D.C., USA. (https://scholar.googleusercontent.com/scholar?q=cache:GubDHo_0IyGJ:scholar.google.com/+Strengthening+America%E2%80%9999s+hunting+heritage+and+wildlife+conservation+in+the+21st+century&hl=en&as_sdt=0,5).
- Stephenson, T. R., V. C. Bleich, B. M. Pierce, and G. P. Mulcahy. 2002. Validation of mule deer body composition using *in vivo* and post-mortem indices of nutritional condition. *Wildlife Society Bulletin* 30:557–564.
- Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. *Canadian Journal of Zoology* 76:717–722.
- Stussy, R. J. 1993. The effects of forage improvement practices on Roosevelt elk in the Oregon Coast range. Thesis, Oregon State University, Corvallis, USA.
- Swanson, M. E., N. M. Studevant, J. L. Campbell, and D. C. Donato. 2014. Biological associates of early-seral pre-forest in the Pacific Northwest. *Forest Ecology and Management* 324:160–171.
- Tarrant, R. F., and R. E. Miller. 1963. Accumulation of organic matter and soil nitrogen beneath a plantation of red alder and Douglas fir. *Soil Science Society of America Proceedings* 27:231–234.
- Thomas, J. W. 1982. Needs for and approaches to wildlife habitat assessment. *Transactions of the North American Wildlife and Natural Resources Conference* 47:35–46.
- Thomas, J. W., D. A. Leckenby, M. G. Henjum, R. Pedersen, and L. D. Bryant. 1988. Habitat-effectiveness index for elk on Blue Mountains winter ranges. U.S. Department of Agriculture, Forest Service, General Technical Report 218, Portland, Oregon, USA.
- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecological Applications* 9:864–879.
- Trainer, C. E. 1971. The relationship of physical condition and fertility of female Roosevelt elk (*Cervus canadensis roosevelti*) in Oregon. Thesis, Oregon State University, Corvallis, Oregon, USA.
- Trudell, J., and R. G. White. 1981. The effect of forage structure and availability on food intake, biting rate, bite size, and daily eating time of reindeer. *Journal of Applied Ecology* 18:63–81.
- Turner, M. G., Y. Wu, L. L. Wallace, W. H. Romme, and A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications* 4:472–496.
- U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management. 1994a. Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service, Portland, Oregon, and USDI Bureau of Land Management, Moscow, Idaho, USA.
- U.S. Department of Agriculture [USDA] Forest Service and U.S. Department of the Interior [USDI] Bureau of Land Management. 1994b. Record of Decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl and standards and guidelines for management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service, Portland, Oregon, and USDI Bureau of Land Management, Moscow, Idaho, USA.
- Van Horne, B., T. A. Hanley, R. G. Cates, J. D. McKendrick, and J. D. Horner. 1988. Influence of seral stage and season on leaf chemistry of southeastern Alaska deer forage. *Canadian Journal of Forestry Research* 18:90–99.
- van Langevelde, F., M. Drescher, I. M. A. Heitkönig, and H. H. T. Prins. 2008. Instantaneous intake rate of herbivores as function of forage quality and mass: effects on facilitative and competitive interactions. *Ecological Modelling* 213:273–284.
- Van Soest, P. J. 1994. Nutritional ecology of the ruminant. Cornell University Press, Ithaca, New York, USA.
- Verbeke, G., and G. Molenberghs. 2000. Linear mixed models for longitudinal data. Springer-Verlag, New York, New York, USA.
- Verme, L. J., and J. J. Ozoga. 1980. Effects of diet on growth and lipogenesis in deer fawns. *Journal of Wildlife Management* 44:315–324.
- Wairimu, S., and R. Hudson. 1993. Foraging dynamics of wapiti stags (*Cervus elaphus*) during compensatory growth. *Applied Animal Behaviour Science* 36:65–79.
- Wakelyn, L. A. 1987. Analysis and comparison of existing and bighorn sheep ranges in Colorado. *Journal of Wildlife Management* 51:904–912.
- Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. *Journal of Range Management* 30:122–127.
- Washington Department of Fish and Wildlife. 2006. Mount St. Helens elk herd plan. Wildlife Management Program, Washington Department of Fish and Wildlife, Olympia, USA.
- Watkins, B. E., R. J. Hudson, and P. L. Fargey. 1991. Compensatory growth of wapiti on aspen parkland ranges. *Canadian Journal of Zoology* 69:1682–1688.

- Weisberg, P. J., and R. J. Swanson. 2003. Regional synchronicity in fire regimes in western Oregon and Washington, USA. *Forest Ecology and Management* 172:17–28.
- West, P. W. 2004. *Tree and forest measurement*. Springer, New York, New York, USA.
- Weston, R. H., and D. P. Poppi. 1987. Comparative aspects of food intake. Pages 133–161 in J. B. Hacker and J. H. Ternouth, editors. *The nutrition of herbivores*. Academic Press, Sydney, Australia.
- White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. *Journal of Wildlife Management* 74:355–369.
- White, P. J., R. A. Garrott, J. J. Borkowski, K. L. Hamlin, and J. G. Berardinelli. 2009. Elk nutrition after wolf recolonization of central Yellowstone. Pages 477–488 in R. A. Garrott, P. J. White, and F. G. R. Watson, editors. *The ecology of large mammals in Central Yellowstone: sixteen years of integrated field studies*. Academic Press, San Diego, California, USA.
- White, P. J., R. A. Garrott, K. L. Hamlin, R. C. Cook, J. G. Cook, and J. A. Cunningham. 2011. Body condition and pregnancy in northern Yellowstone elk – evidence for predation risk effects? *Ecological Applications* 21:3–8.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377–384.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parrish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285–1301.
- Wilmschurst, J. F., J. M. Fryxell, and P. E. Colucci. 1999. What constrains daily intake in Thompson's gazelles? *Ecology* 80:2338–2347.
- Wisdom, M. J., L. R. Bright, C. G. Carey, W. W. Hines, R. J. Pedersen, D. A. Smithey, J. W. Thomas, and G. W. Witmer. 1986. *A model to evaluate elk habitat in western Oregon*. U.S. Department of Agriculture, Forest Service, Publication R6-F&WL-216-1986, Portland, Oregon, USA.
- Wisdom, M. J., J. G. Cook, M. W. Rowland, and J. H. Noyes. 1993. *Protocols for care and handling of deer and elk at the Starkey Experimental Forest and Range*. U.S. Department of Agriculture, Forest Service, General Technical Report PNW-GTR-311, Pacific Northwest Forestry and Range Laboratory, La Grande, Oregon, USA.
- Yarrow, G. K. 1979. *Comparison of tame and wild deer food habits*. Thesis, Mississippi State University, Starkville, USA.

APPENDIX A. Estimating tannin astringency and gross energy (GE) content of plant life-form groups (graminoids, forbs, evergreen shrubs, deciduous shrubs, and forest ferns).

Our nutritional assays of plant life-form groups included only detergent fiber analyses, and thus did not include effects of tannin astringency nor provide estimates of GE needed to convert estimates of dry matter digestibility (DMD) to digestible energy (DE, kcal/g of forage) with influences of tannins incorporated. We derived estimates of GE and tannins using our elk diet samples, which were multi-species composite samples, where amount of each plant species was in proportion to that in elk diets. We selected among all of our elk diet samples to identify those that consisted of >80% of any 1 of the plant life-form groups. From these, we calculated mean BSA and GE for each plant life-form group by study area, and used the means as constants reflecting tannin effects and GE in equations of Robbins et al. (1987*a, b*) to estimate DMD and DE for each plant life-form group.

We used ANCOVA to identify significant differences in tannin astringency and GE from our elk diet samples with study area, plant life-form group, their interaction, date of sample collection, and the interaction of date and plant group. We excluded graminoids from the tannin ANCOVA because they lack tannins (Cook 2002, Robbins 1983). We reran the ANCOVAs as 2-factor ANOVAs if the covariates representing date effects were insignificant. We then used means by study area and plant groups, adjusted by date if necessary, to calculate forage DE by plant life-form group that reflected tannin effects and GE levels.

We identified 254 diet samples collected over all days of pen occupancy with >80% deciduous shrubs, 44 with >80% forbs, 32 with >80% evergreen shrubs, and none with more than 15% ferns. Neither the date of sample collection, nor the interaction of date and plant groups significantly influenced tannin astringency ($P > 0.48$), and we reran the analysis as a 2-factor ANOVA and used Student Newman–Keuls multiple range test to identify differences among plant groups and study area. Precipitation of BSA differed among study areas (lowest at Willapa Hills, $P = 0.020$; study area-plant group interaction: $P = 0.90$) but was similar among forbs, deciduous shrubs, and evergreen shrubs (Fig. A1). Lopez (2006) reported for an area immediately north of our Willapa Hills study area that tannin astringency of ferns was similar to that of deciduous and evergreen shrubs, using the same laboratory procedures that we used. Thus, we used the average of forbs, deciduous, and evergreen shrubs for all forage classes, excluding graminoids, but included different estimates of tannin astringency for Willapa Hills (0.0424) versus Nooksack and Springfield (0.0595 mg of BSA precipitated/mg foliage) for calculating DE of forage quality samples. Based on equations of Robbins et al. (1987*a, b*), a 50% over- or underestimate of BSA precipitation (e.g., 0.06 vs. 0.09 mg BSA/mg foliage) changes estimates of DMD only by 1 percentage point, illustrating that relatively large errors in estimates of tannin astringency had small effects on estimates of DMD and DE.

We assayed GE only for samples collected the first day of pen occupancy by elk in the macroplots, thus providing fewer samples for GE analysis ($n = 90$ diet samples meeting our criteria of having >80% of 1 of the plant life-form groups). Six of 12 study area-plant group cells in the ANCOVA contained <3 samples, and influences of date of collection were minor ($P > 0.07$), so we conducted our analysis with plant group as levels (evergreen shrubs, deciduous shrubs, forbs, and graminoids) in a 1-way ANOVA. Gross energy of evergreen shrubs was greater than that of graminoids and forbs ($P = 0.035$): 4.80 ± 0.147 , 4.60 ± 0.024 , 4.50 ± 0.123 , and 4.50 ± 0.049 kcal/g of foliage ($\bar{x} \pm \text{SE}$) for evergreen shrubs, deciduous shrubs, graminoids, and forbs, respectively. We used a value of 4.80 for evergreen shrubs and assumed that GE of the other plant groups including ferns was equivalent at 4.53 kcal/g of foliage, the mean of the other plant groups, for calculating DE of forage quality samples.

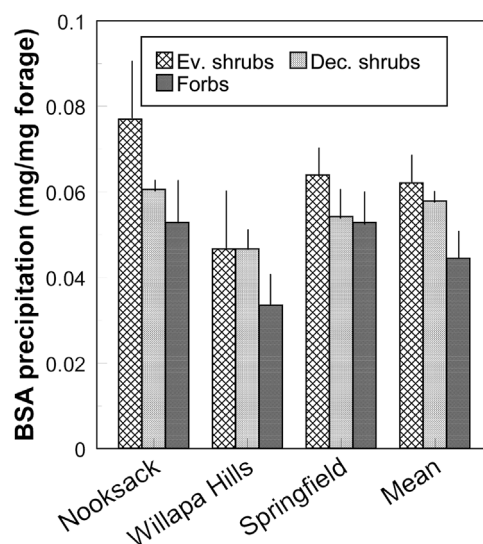


Figure A1. Bovine serum albumin (BSA) precipitation (a measure of tannin astringency) of evergreen (ev.) shrubs, deciduous (dec.) shrubs, and forbs at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

APPENDIX B.

Table B1. Equations relating stand age (age) to overstory canopy cover (cc, %) in 5 habitat types for the Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

Study area ^a	Habitat type ^b	Stand age (yr)	Equation	<i>n</i>	<i>S_{y·x}</i> ^c	<i>r</i> ²	<i>P</i>	Method ^d
Nk	WHS, combined	1–75	$cc = 92.9 / (1 + 20.66 e^{(-0.2504(\text{age}))})$	55	15.84	0.86	<0.001	GN
	PSS	1–75	$cc = 90.5 / (1 + 304.6 e^{(-0.2019(\text{age}))})$	27	6.60	0.98	<0.001	GN
	MHS	1–75	$cc = 74.9 / (1 + 144.3 e^{(-0.2030(\text{age}))})$	15	13.54	0.77	<0.001	GN
	Hardwood	1–75	$cc = 87.9 \pm 7.45\%$	8		0.75		LS
WH	WHS, combined	1–75	$cc = 92.0 / (1 + 3476.3 e^{(-0.7956(\text{age}))})$	75	6.79	0.99	<0.001	GN
	PSS	1–75	No analysis attempted	7				
Sp	WHS-salal	1–75	$cc = 89.4 / (1 + 170.0 e^{(-0.3768(\text{age}))})$	53	13.56	0.89	<0.001	GN
	WHS-swordfern	1–75	$cc = 90.1 / (1 + 452.2 e^{(-0.4572(\text{age}))})$	30	4.20	0.99	<0.001	GN
	WHS, combined	1–75	$cc = 89.7 / (1 + 209.4 e^{(-0.3928(\text{age}))})$	83	11.12	0.92	<0.001	GN
	PSS	1–75	No analysis attempted	7				
Comb	WHS, combined	8–650	$cc = 94.6 - 0.027(\text{age}) - 5,332.76(1/\text{age}^2)$	172	14.56	0.72	<0.001	LS
	WHS, combined	50–650	$cc = 91.8 - 0.021(\text{age})$	57	6.06	0.25	<0.001	LS
	PSS	1–75	$cc = 89.2 / (1 + 219.5 e^{(-0.2335(\text{age}))})$	36	10.85	0.94	<0.001	GN
	PSS	8–500	$cc = 92.7 - 0.048(\text{age}) - 14,549.4(1/\text{age}^2)$	31	15.81	0.80	<0.001	LS
	PSS	50–500	$cc = 91.5 - 0.048(\text{age})$	13	9.42	0.40	0.020	LS
	MHS	1–500	No analysis attempted	23				

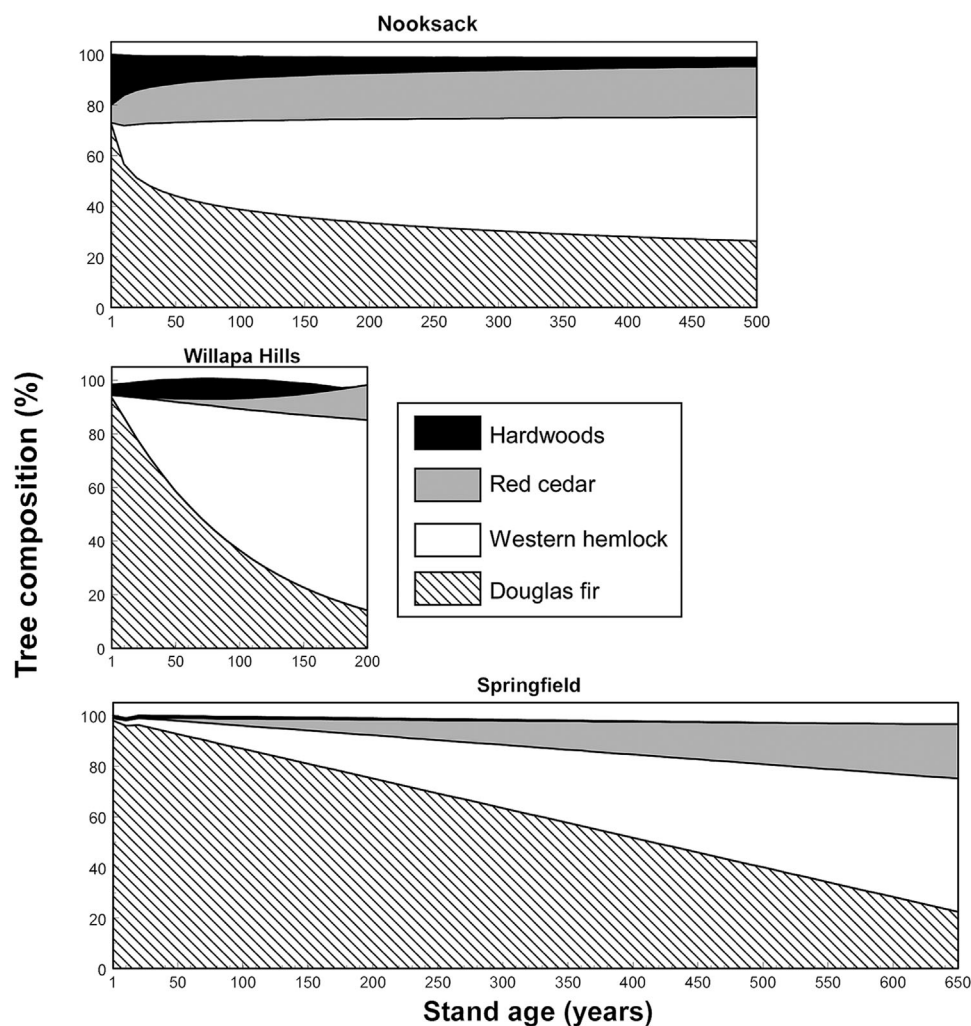
^a Study area codes are Nk = Nooksack; WH = Willapa Hills; Sp = Springfield; Comb = all study areas.

^b Habitat codes are WHS = western hemlock series; PSS = Pacific silver fir series; MHS = mountain hemlock series; WHS-salal = salal plant association in WHS; WHS-swordfern = swordfern plant association in the WHS; and hardwood = alder dominated hardwood.

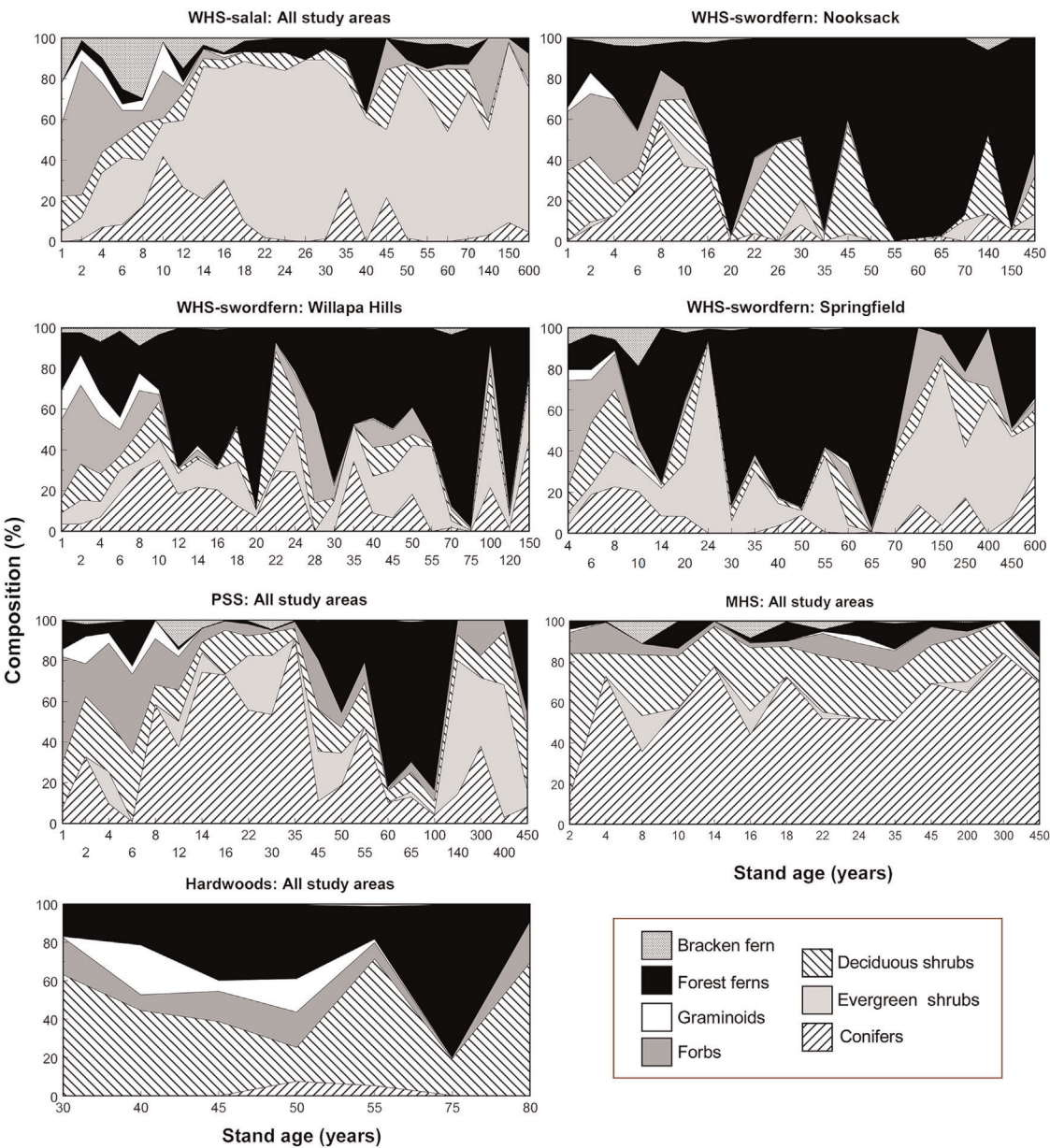
^c *S_{y·x}* = standard error of the estimate.

^d Model estimation method: GN = Gauss–Newton; LS = least squares.

APPENDIX C. Development of overstory tree composition during succession in the western hemlock series (WHS) at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Douglas fir declined ($r^2 = 0.11$ – 0.42 ; $P < 0.001$ – 0.01) and western hemlock increased ($r^2 = 0.19$ – 0.34 ; $P < 0.001$) with stand age at all 3 study areas; western red cedar increased at Willapa Hills and Springfield ($r^2 = 0.18$ – 0.19 ; $P \leq 0.001$); and hardwoods significantly declined only at Willapa Hills ($r^2 = 0.20$; $P < 0.001$). In the Pacific silver fir series (PSS) and mountain hemlock series (MHS), we found no significant changes in tree composition, except for increases in mountain hemlock in the MHS ($r^2 = 0.20$; $P = 0.046$). These data provide additional evidence that plant succession occurs more rapidly at Willapa Hills than at Nooksack or Springfield.



APPENDIX D. Successional changes in understory composition of plant life-form groups in the western hemlock series (WHS)-swordfern habitat type at Nooksack, Willapa Hills, and Springfield; and across all study areas in the western hemlock series (WHS)-salal, Pacific silver fir series (PSS), mountain hemlock series (MHS), and hardwood stands in the WHS in western Oregon and Washington, 2000–2002. Graphs exclude data from thinned stands.



APPENDIX E.

Table E1. Ivlev and Chesson selectivity indices, sample size (*n*), percent of diets (for pens where the species was present), bite mass (for pens where species was eaten), and selection category (S = significantly selected, A = significantly avoided, and N = neither selected nor avoided) of plant species in elk foraging trials at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. We classed hardwood trees as deciduous shrubs for diet composition and selection analyses. Plant names are from Hitchcock and Cronquist (1973) and ordered first by forage selection category and second alphabetically by scientific name.

Scientific name ^a	Plant group ^b	Plant species	Common name	<i>n</i>	Ivlev	Chesson	Diet (%)	Bite mass (g)		Selection
								\bar{x}	SE	
<i>Acer circinatum</i>	DS	ACCI	Vine maple	62	0.626	0.091	11.4	0.429	0.031	S
<i>Acer macrophyllum</i>	DS	ACMA	Big leaf maple	28	0.474	0.102	4.9	0.977	0.098	S
<i>Alnus incana</i>	DS	ALIN	Mountain alder	1	0.875	0.076	1.5	0.687		S
<i>Alnus rubra</i>	DS	ALRU	Red alder	36	0.232	0.033	1.7	0.566	0.046	S
<i>Anaphalis margaritacea</i>	Fb	ANMA	Pearly everlasting	48	0.272	0.025	1.9	0.439	0.026	S
<i>Bryoria</i> spp. ^c	NV	BRYO	Arboreal lichen	10			3.8	0.466	0.069	S
<i>Buddleja davidii</i>	DS	BUDA	Butterflybush	11	0.435	0.079	1.7	0.578	0.074	S
<i>Calamagrostis canadensis</i>	Gr	CACA	Bluejoint reedgrass	1	0.966	0.231	5.8	0.702		S
<i>Carex</i> spp.	Gr	CARE	Sedge	70	0.237	0.043	2.1	0.532	0.034	S
<i>Cinna latifolia</i>	Gr	CILA	Woodreed	1	0.936	0.053	3.0	0.51		S
<i>Clintonia uniflora</i>	Fb	CLUUN	Queen's cup beadlily	13	0.800	0.109	14.5	0.412	0.023	S
<i>Corylus cornuta</i>	DS	COCO	Marsh hazelnut	24	0.571	0.074	4.6	0.572	0.073	S
<i>Galeopsis tetrahit</i>	Fb	GATE	Common hemp nettle	2	0.550	0.008	0.4	0.580		S
<i>Hypericum perforatum</i>	Fb	HYPE	Common St. John's-wort	18	0.222	0.015	1.1	0.410	0.048	S
<i>Hypochaeris radicata</i>	Fb	HYRA	Spotted cats-ear	25	0.340	0.057	5.5	0.245	0.024	S
<i>Iris tenax</i>	Fb	IRTE	Oregon iris	32	0.540	0.038	5.5	0.515	0.042	S
<i>Ligusticum apiifolium</i>	Fb	LIAP	Celery-leaved lovage	1	0.974	0.163	7.7	0.255	0.075	S
<i>Linnaea borealis</i>	ES	LIBO	Western twinflower	13	0.506	0.030	2.9	0.406	0.047	S
<i>Lolium perenne</i>	Gr	LOPE	English ryegrass	1	0.954	0.136	4.2	1.110		S
<i>Lonicera ciliosa</i>	DS	LOCI	Trumpet honeysuckle	4	0.565	0.028	1.2	0.577	0.187	S
<i>Luzula</i> spp.	Gr	LUZU	Woodrush	43	0.192	0.033	4.2	0.453	0.033	S
<i>Maianthemum dilatatum</i>	Fb	MADI	Beadruby	16	0.499	0.104	6.8	0.115	0.018	S
<i>Basidiomycota</i> ^c	NV	MUSH	Mushrooms, conks	14			0.1	0.043	0.009	S
<i>Oplopanax horridum</i>	DS	OPHO	Devil's club	12	0.526	0.08	4.7	0.512	0.056	S
<i>Oxalis oregana</i>	Fb	OXOR	Oregon oxalis	13	0.671	0.109	9.2	0.073	0.008	S
<i>Pedicularis</i> spp.	Fb	PEDI	Lousewort	1	0.868	0.021	8.5	0.600		S
<i>Petasites frigidus</i>	Fb	PEFR	Sweet coltsfoot	6	0.524	0.059	1.5	0.803	0.165	S
<i>Phalaris arundinacea</i>	Gr	PHAR	Reed canarygrass	4	0.903	0.104	4.8	0.328	0.072	S
<i>Phleum pratense</i>	Gr	PHPR	Common timothy	1	0.846	0.024	1.2	0.810		S
<i>Pyrus communis</i>	DS	PYCO	Cult pear	1	0.984	0.248	12.3	0.397		S
<i>Pyrus fusca</i>	DS	PYFU	Western crabapple	1	0.857	0.034	1.3	0.395		S
<i>Rhamnus purshiana</i>	DS	RHPU	Cascara	24	0.329	0.046	1.7	0.642	0.056	S
<i>Ribes sanguineum</i>	DS	RISA	Red currant	21	0.272	0.038	3.0	0.398	0.086	S
<i>Rubus parviflorus</i>	DS	RUPA	Thimbleberry	45	0.191	0.030	8.4	0.501	0.034	S
<i>Salix</i> spp.	DS	SALI	Willow	16	0.647	0.086	4.2	0.679	0.067	S
<i>Smilicina</i> spp.	Fb	SMIL	Solomon-plume	10	0.368	0.038	1.4	0.260	0.048	S
<i>Sorbus sitchensis</i>	DS	SOSI	Sitka mountain-ash	11	0.871	0.109	10.7	0.738	0.091	S
<i>Spiraea douglasii</i>	DS	SPDO	Douglas spirea	8	0.666	0.142	4.1	0.527	0.075	S
<i>Symphoricarpos</i> spp.	DS	SYMP	Snowberry	38	0.487	0.053	6.5	0.235	0.026	S
<i>Tofieldia glutinosa</i>	Fb	TOGL	Sticky tofieldia	1	0.778	0.016	0.8	0.270		S
<i>Trifolium</i> spp.	Fb	TRIF	Clover	4	0.730	0.152	9.0	0.426	0.018	S
<i>Vaccinium parvifolium</i>	DS	VAPA	Red bilberry	72	0.559	0.138	10.4	0.607	0.047	S
<i>Valeriana sitchensis</i>	Fb	VASI	Sitka valerian	4	0.534	0.064	2.3	0.243	0.041	S
<i>Achlys triflora</i>	Fb	ACTR	Vanilla leaf	8	0.275	0.014	1.2	0.216	0.028	N
<i>Adenocaulon bicolor</i>	Fb	ADBI	Trail plant	14	0.189	0.013	0.9	0.347	0.040	N
<i>Adiantum pedatum</i>	Fn	ADPE	Maidenhair fern	7	−0.197	0.038	0.7	0.566	0.116	N
<i>Agrostis exarata</i>	Gr	AGEX	Spike bentgrass	11	−0.029	0.008	1.5	0.656	0.088	N
<i>Agrostis</i> spp.	Gr	AGRO	Bentgrass	32	0.199	0.06	3.6	0.865	0.085	N
<i>Alnus sinuata</i>	DS	ALSI	Sitka alder	5	0.265	0.021	5.3	0.808	0.327	N
<i>Amelanchier alnifolia</i>	DS	AMAL	Western serviceberry	4	0.174	0.021	1.1	0.253	0.090	N
<i>Anemone deltoidea</i>	Fb	ANDE	Threelobed windflower	5	−0.190	0.005	0.2	0.211	0.036	N
<i>Angelica genuflexa</i>	Fb	ANGE	Kneeling Angelica	1	0.000	0.006	0.3	0.210		N
<i>Antennaria</i> spp.	Fb	ANTE	Everlasting	1	0.000	0.004	0.1	0.470		N
<i>Arctostaphylos columbiana</i>	ES	ARCO	Bristly manzanita	5	−0.267	0.006	0.1	0.740	0.064	N
<i>Arenaria macrophylla</i>	Fb	ARMA	Bigleaf sandwort	2	0.741	0.132	1.0	0.131		N
<i>Artemisia suksdorfii</i>	Fb	ARSU	Coastal mugwort	1	0.000	0.002	0.2	0.500		N
<i>Aruncus sylvestris</i>	Fb	ARSY	Goatsbeard	2	−0.200	0.003	0.2	0.795		N
<i>Asarum caudatum</i>	Fb	ASCA	Wild ginger	6	−0.221	0.004	0.3	0.184	0.023	N
<i>Astragalus</i> spp.	Fb	ASTR	Locoweed	3	−0.444	0.008	0.7	0.397	0.088	N
Attached leaf lichens ^{c,d}	NV	ALLI		13			0.4	0.423	0.067	N

(Continued)

Table E1. (Continued)

Scientific name ^a	Plant group ^b	Plant species	Common name	n	Ivlev	Chesson	Diet (%)	Bite mass (g)		
								\bar{x}	SE	Selection
<i>Bromus vulgaris</i>	Gr	BRVU	Columbia brome	41	0.047	0.042	2.3	0.443	0.044	N
<i>Campanula scouleri</i>	Fb	CASC	Scouler's harebell	17	-0.175	0.006	0.2	0.130	0.036	N
<i>Castanopsis chrysophylla</i>	ES	CACH	Chinquapin	8	0.024	0.022	0.8	0.541	0.072	N
<i>Chrysanthemum leucanthemum</i>	Fb	CHLE	Chrysanthemum	20	-0.181	0.004	0.6	0.197	0.023	N
	Fb	CIRS	Thistle	36	0.071	0.016	4.0	0.813	0.068	N
<i>Cornus canadensis</i>	DS	COCA	Bunchberry dogwood	13	-0.018	0.016	2.0	0.224	0.023	N
<i>Cornus nuttallii</i>	DS	CONU	Pacific dogwood	2	0.778	0.087	2.4	0.360		N
<i>Cornus stolonifera</i>	Fb	COST	Red-osier dogwood	1	0.333	0.011	0.2	0.514		N
<i>Crepis</i> spp.	Fb	CREP	Hawksbeard	11	-0.232	0.004	0.3	0.227	0.028	N
<i>Cytisus scoparius</i>	DS	CYSC	Scot's broom	3	-0.333	0.005	0.1	0.210	0.015	N
<i>Dactylis glomerata</i>	Gr	DAGL	Orchard-grass	5	0.541	0.125	6.3	1.241	0.210	N
<i>Daucus carota</i>	Fb	DACA	Wild carrot	3	0.489	0.047	0.6	0.320	0.020	N
<i>Dianthus armeria</i>	Fb	DIAR	Grass pink	2	-0.500	0.001	0.1	0.440		N
<i>Dicentra formosa</i>	Fb	DIFO	Pacific bleedingheart	14	0.170	0.027	0.7	0.167	0.013	N
<i>Disporum</i> spp.	Fb	DISP	Fairy-bell	19	-0.008	0.010	0.4	0.177	0.013	N
<i>Dryopteris austriaca</i>	Fb	DRAU	Mountain wood-fern	18	-0.113	0.014	0.4	0.435	0.063	N
<i>Elymus glaucus</i>	Gr	ELGL	Blue wildrye	16	-0.179	0.017	1.1	0.452	0.137	N
<i>Elymus</i> spp.	Gr	ELYM	Wildrye	40	-0.046	0.047	2.7	0.443	0.055	N
<i>Epilobium angustifolium</i>	Fb	EPAN	Fireweed	46	0.117	0.028	9.3	0.754	0.058	N
<i>Equisetum</i> spp.	Gr	EQUI	Horsetail	10	-0.106	0.013	2.0	1.623	0.229	N
<i>Festuca occidentalis</i>	Gr	FEOC	Western fescue	13	-0.295	0.004	0.1	0.730	0.175	N
<i>Festuca subulata</i>	Gr	FESU	Bearded fescue	3	-0.115	0.004	0.8	0.300	0.030	N
<i>Fragaria vesca</i>	Fb	FRVE	Woods strawberry	5	-0.666	0.002	1.0	0.130	0.075	N
<i>Galium oreganum</i>	Fb	GAOR	Oregon bedstraw	4	0.257	0.018	0.6	0.092	0.022	N
<i>Galium triflorum</i>	Fb	GATR	Sweetscented bedstraw	40	0.048	0.015	2.2	0.190	0.029	N
<i>Geum macrophyllum</i>	Fb	GEMA	Oregon avens	4	-0.600	0.002	0.1	0.180	0.021	N
<i>Glyceria elata</i>	Gr	GLEL	Tall mannagrass	7	0.187	0.036	3.5	0.500	0.083	N
<i>Glyceria</i> spp.	Gr	GLYC	Mannagrass	1	0.333	0.004	0.2	0.170		N
<i>Gymnocarpium dryopteris</i>	Fb	GYDR	Oak-fern	3	0.133	0.006	0.3	0.249	0.051	N
<i>Hieracium albiflorum</i>	Fb	HAL	White-flowered hawkweed	16	0.000	0.042	2.1	0.336	0.019	N
<i>Holcus lanatus</i>	Gr	HOLA	Common velvet grass	34	0.120	0.026	5.4	0.491	0.046	N
<i>Holodiscus discolor</i>	DS	HODI	Creambush ocean-spray	23	0.226	0.035	2.2	0.370	0.043	N
<i>Hydrophyllum fendleri</i>	Fb	HYFE	Fendler's waterleaf	2	0.000	0.004	0.1	0.151		N
<i>Juncus</i> spp.	Gr	JUNC	Rush	9	-0.369	0.007	0.2	0.497	0.035	N
<i>Lactuca muralis</i>	Fb	LAMU	Wall Lettuce	36	0.029	0.032	4.7	0.150	0.013	N
<i>Lathyrus</i> spp.	Fb	LATH	Peavine	9	0.254	0.015	0.5	0.691	0.123	N
<i>Lilium columbianum</i>	Fb	LICO	Tiger lily	3	0.167	0.038	0.8	0.420	0.005	N
<i>Lupinus</i> spp.	Fb	LUPI	Lupine	5	-0.115	0.004	0.3	0.251	0.009	N
<i>Lysichitum americanum</i>	Fb	LYAM	Skunk cabbage	5	0.339	0.010	4.9	0.431	0.147	N
<i>Melica bulbosa</i>	Gr	MEBU	Oniongrass	1	-0.739	0.003	0.3	1.390		N
<i>Mimulus moschatatus</i>	Fb	MIMO	Musk-flower	1	0.000	0.002	0.1	0.080		N
<i>Monotropa uniflora</i>	Fb	MOUN	Indian-pipe	3	0.367	0.010	0.3	0.630	0.270	N
<i>Montia sibirica</i>	Fb	MOSI	Western springbeauty	15	-0.176	0.012	0.4	0.148	0.028	N
<i>Oemleria cerasiformis</i>	DS	OECE	Indian plum	7	0.16	0.022	0.5	0.500	0.092	N
<i>Penstemon</i> spp.	Fb	PENS	Beardtongue	7	-0.105	0.014	1.4	0.448	0.131	N
<i>Phacelia hastata</i>	Fb	PHHA	Whiteleaf phacelia	1	-1.000	0.000	0.0			N
<i>Plantago</i> spp.	Fb	PLAN	Plantain	4	-0.017	0.007	0.2	0.238	0.014	N
<i>Poa compressa</i>	Gr	POCO	Canadian bluegrass	3	0.059	0.009	0.4	0.56	0.125	N
<i>Populus trichocarpa</i>	DS	POTR	Black cottonwood	3	-0.012	0.080	1.9	0.588	0.128	N
<i>Prunus emarginata</i>	DS	PREM	Bittercherry	27	0.045	0.013	1.4	0.314	0.027	N
<i>Ranunculus</i> spp.	Fb	RANU	Buttercup	2	-0.030	0.032	1.6	0.164	0.041	N
<i>Ribes bracteosum</i>	DS	RIBR	Stink currant	2	-0.063	0.003	0.4	0.760	0.120	N
<i>Ribes divaricatum</i>	DS	RIDI	Straggly gooseberry	8	-0.377	0.008	0.2	0.278	0.033	N
<i>Ribes lacustre</i>	DS	RILA	Swamp gooseberry	1	0.000	0.0055	0.1	0.220		N
<i>Ribes</i> spp.	DS	RIBE	Currant	1	-1.000	0.000	0.0	0.180		N
<i>Rosa gymnocarpa</i>	DS	ROGY	Baldhip rose	34	0.044	0.025	0.8	0.167	0.018	N
<i>Rubus nivalis</i>	DS	RUNI	Snow bramble	3	-0.615	0.001	0.1	0.177	0.043	N
<i>Rubus pedatus</i>	DS	RUPE	Fiveleaved bramble	9	-0.445	0.005	0.4	0.129	0.017	N
<i>Rubus spectabilis</i>	DS	RUSP	Salmonberry	44	-0.047	0.017	9.0	0.521	0.025	N
<i>Rumex occidentalis</i>	Fb	RUOC	Western dock	3	-0.556	0.001	0.1	0.191	0.001	N
<i>Rumex acetosella</i>	Fb	RUME	Sheep sorrel	13	-0.013	0.012	0.4	0.291	0.034	N
<i>Sambucus</i> spp.	DS	SAMB	Elderberry	38	0.076	0.061	2.7	0.63	0.052	N
<i>Satureja douglasii</i>	Fb	SADO	Yerba Buena	1	0.000	0.005	0.1	0.420		N
<i>Scutellaria galericulata</i>	Fb	SCGA	Marsh skullcap	5	-0.033	0.059	2.7	0.430	0.050	N
<i>Scutellaria lateriflora</i>	Fb	SCLA	Mad-dog skullcap	2	-0.073	0.002	0.8	0.320		N
<i>Senecio sylvaticus</i>	Fb	SESY	Wood groundsel	6	0.037	0.011	0.4	0.647	0.029	N
<i>Senecio triangularis</i>	Fb	SETR	Arrowleaf groundsel	4	0.337	0.021	0.4	0.256	0.033	N

(Continued)

Table E1. (Continued)

Scientific name ^a	Plant group ^b	Plant species	Common name	n	Ivlev	Chesson	Diet (%)	Bite mass (g)		
								\bar{x}	SE	Selection
<i>Solidago canadensis</i>	Fb	SOCA	Canadian goldenrod	6	-0.056	0.004	0.2	0.446	0.144	N
<i>Sonchus asper</i>	Fb	SOAS	Prickly sow-thistle	5	0.110	0.010	0.2	0.260	0.045	N
<i>Sorbus aucuparia</i>	DS	SOAU	European mountain-ash	4	0.054	0.012	0.0	0.600	0.053	N
<i>Stachys cooleyae</i>	Fb	STCO	Cooley's hedge-nettle	2	0.614	0.033	1.1	0.185	0.005	N
<i>Stellaria</i> spp.	Fb	STEL	Starwort	30	-0.008	0.010	0.4	0.427	0.070	N
<i>Streptopus roseus</i>	Fb	STRO	Rosy twisted-stalk	4	0.248	0.021	0.7	0.108	0.009	N
<i>Synthyris reniformis</i>	Fb	SYRE	Snow-queen	2	-0.333	0.005	0.1	0.040		N
<i>Taraxacum</i> spp.	Fb	TARA	Dandelion	3	-0.333	0.003	0.1	0.251	0.022	N
<i>Thalictrum occidentale</i>	Fb	THOC	Western meadowrue	1	0.000	0.001	0.1	0.053		N
<i>Tiarella trifoliata</i>	Fb	TITR	Coolwort foamflower	18	-0.168	0.035	1.1	0.212	0.041	N
<i>Tolmiea menziesii</i>	Fb	TOME	Youth-on-age	10	-0.354	0.007	1.8	0.327	0.035	N
<i>Trillium</i> spp.	Fb	TRIL	Wake-robin	6	-0.417	0.003	0.1	0.111	0.007	N
<i>Trisetum cernuum</i>	Gr	TRCE	Nodding trisetum	5	-0.250	0.058	1.0	1.372	0.017	N
<i>Typha latifolia</i>	Gr	TYLA	Common cat-tail	1	0.857	0.106	1.3	1.110		N
<i>Vaccinium alaskaense/ovalifolium</i>	DS	VALOV	Huckleberry	23	0.290	0.055	21.2	0.751	0.058	N
<i>Vaccinium membranaceum</i>	DS	VAME	Big huckleberry	6	-0.963	0.000	0.0	0.590	0.051	N
<i>Vancouveria hexandra</i>	Fb	VAHE	White inside-out-flower	21	0.059	0.017	0.8	0.123	0.009	N
<i>Veratrum viride</i>	Fb	VEVI	American false hellebore	7	0.035	0.007	0.3	0.631	0.150	N
<i>Veronica officinalis</i>	Fb	VEOF	Common speedwell	12	0.011	0.023	0.8	0.455	0.057	N
<i>Vicia</i> spp.	Fb	VICI	Vetch	3	-0.394	0.015	0.3	0.270	0.040	N
<i>Viola</i> spp.	Fb	VIOL	Violet	44	-0.165	0.010	0.6	0.166	0.015	N
<i>Xerophyllum tenax</i>	Fb	XETE	Indian basket grass	2	-0.727	0.001	1.8	2.230		N
<i>Abies amabilis</i>	Cn	ABAM	Pacific silver fir	11	-1.000	0.000	0.0	0.900	0.000	A
<i>Abies procera</i>	Cn	ABPR	Noble fir	4	-1.000	0.000	0.0	0.000	0.000	A
<i>Arbutus menziesii</i>	ES	ARME	Pacific madrone	1	-0.412	0.004	0.5	1.450		A
<i>Athyrium filix-femina</i>	Fn	ATFI	Lady-fern	25	-0.255	0.008	1.7	0.551	0.061	A
<i>Berberis nervosa</i>	ES	BENE	Oregon grape	64	-0.678	0.005	1.3	0.634	0.029	A
<i>Blechnum spicant</i>	Fn	BLSP	Deer-fern	17	-0.920	0.000	0.1	0.367	0.033	A
<i>Ceanothus velutinus</i>	ES	CEVE	Snowbrush ceanothus	8	-0.500	0.005	1.9	0.514	0.108	A
<i>Chimaphila menziesii</i>	ES	CHME	Little pipsissewa	2	-1.000	0.000	0.0	0.080		A
<i>Circaea alpine</i>	Fb	CIAL	Enchanters nightshade	5	-0.800	0.000	0.0	0.110	0.009	A
<i>Deschampsia elongata</i>	Gr	DEEL	Slender hairgrass	15	-0.448	0.005	0.4	0.564	0.100	A
<i>Digitalis purpurea</i>	Fb	DIPU	Foxglove	18	-0.952	0.000	0.1	0.319	0.015	A
<i>Epilobium paniculatum</i>	Fb	EPPA	Autumn willow-weed	8	-0.521	0.003	0.1	0.240	0.031	A
<i>Epilobium watsonii</i>	Fb	EPWA	Watson's willow-herb	22	-0.322	0.005	0.6	0.341	0.039	A
<i>Erechtites minima</i>	Fb	ERMI	Toothed coast fireweed	6	-0.448	0.002	0.2	0.304	0.038	A
<i>Gaultheria ovatifolia</i>	ES	GAOV	Slender wintergreen	7	-0.952	0.000	0.1	0.197	0.016	A
<i>Gaultheria shallon</i>	ES	GASH	Salal	54	-0.247	0.035	9.3	0.574	0.037	A
<i>Ilex</i> sp.	ES	ILEX	Holly	3	-0.667	0.002	0.0	0.310	0.028	A
<i>Mentha arvensis</i>	Fb	MIAR	Corn mint	5	-0.600	0.002	0.1	0.080	0.008	A
<i>Menziesia ferruginea</i>	DS	MEFE	Fool's huckleberry	12	-0.887	0.000	0.1	0.408	0.040	A
Clubmoss, liverwort, moss ^c	NV	MOSS		7			0.1	0.491	0.110	A
<i>Nothofelone nemorosa</i>	Fb	NONE	Woodland beard-tongue	1	-0.909	0.000	0.2	0.250		A
<i>Osmorhiza chilensis</i>	Fb	OSCH	Mountain sweet-cicely	6	-0.460	0.001	0.1	0.081	0.001	A
<i>Phyllodoce empetrififormis</i>	ES	PHEM	Red mountain-heath	2	-1.000	0.000	0.0			A
<i>Pinus monticola</i>	Cn	PIMO	White pine	1	-1.000	0.000	0.0	0.600		A
<i>Poa pratensis</i>	Gr	POPR	Kentucky bluegrass	15	-0.699	0.003	0.1	0.245	0.068	A
<i>Poa</i> sp.	Gr	POAS	Bluegrass	8	-0.640	0.006	1.0	0.175	0.075	A
<i>Polystichum munitum</i>	Fn	POMU	Sword-fern	76	-0.874	0.004	0.8	1.385	0.113	A
<i>Prunella vulgaris</i>	Fb	PRVU	Self-heal	7	-0.643	0.001	0.1	0.138	0.007	A
<i>Pseudotsuga menziesii</i>	Cn	PSME	Douglas fir	57	-0.342	0.031	3.1	1.113	0.070	A
<i>Pteridium aquilinum</i>	Fn	PTAQ	Bracken fern	71	-0.122	0.037	6.8	1.297	0.080	A
<i>Pyrola</i> spp.	Fb	PYRO	Pyrola	1	-1.000	0.000	0.0	0.110		A
<i>Rhododendron albiflorum</i>	ES	RHAL	White rhododendron	3	-0.867	0.000	0.1	0.345	0.035	A
<i>Rhododendron macrophyllum</i>	ES	RHMA	Pacific rhododendron	4	-0.883	0.000	0.6	0.770	0.091	A
<i>Rubus discolor</i>	DS	RUDI	Himalayan blackberry	24	-0.305	0.011	2.5	0.569	0.051	A
<i>Rubus laciniatus</i>	ES	RULA	Evergreen blackberry	24	-0.505	0.005	0.5	0.528	0.071	A
<i>Rubus leucodermis</i>	DS	RULE	Black raspberry	24	-0.563	0.002	0.4	0.301	0.023	A
<i>Rubus ursinus</i>	DS	RUUR	Pacific blackberry	80	-0.587	0.003	1.9	0.249	0.012	A
<i>Solanum dulcamara</i>	Fb	SODU	Climbing nightshade	4	-1.000	0.000	0.0	0.410	0.080	A
<i>Tanacetum vulgare</i>	Fb	TAVU	Common tansy	1	-0.778	0.000	0.1	0.210		A
<i>Taxus brevifolia</i>	ES	TABR	Western yew	5	-1.000	0.000	0.0			A
<i>Tellima grandiflora</i>	Fb	TEGR	Fringecup	5	-0.700	0.002	0.1	0.090	0.011	A
<i>Thuja plicata</i>	Cn	THPL	Western red cedar	9	-1.000	0.000	0.0	0.600	0.083	A
<i>Trientalis latifolia</i>	Fb	TRLA	Western starflower	29	-0.412	0.003	0.1	0.117	0.007	A
<i>Tsuga heterophylla</i>	Cn	TSHE	Western hemlock	31	-0.800	0.002	0.1	0.557	0.110	A
<i>Tsuga mertensiana</i>	Cn	TSME	Mountain hemlock	5	-1.000	0.000	0.0			A

(Continued)

Table E1. (Continued)

Scientific name ^a	Plant group ^b	Plant species	Common name	n	Ivlev	Chesson	Diet (%)	Bite mass (g)		
								\bar{x}	SE	Selection
<i>Urtica dioica</i>	Fb	URDI	Stinging nettle	2	-1.000	0.000	0.0	0.245	0.065	A
<i>Veronica americana</i>	Fb	VEAM	American brookline	2	-1.000	0.000	0.0	0.152	0.008	A
<i>Whipplea modesta</i>	Fb	WHMO	Yerba de selva	3	-0.897	0.000	0.1	0.533	0.033	A

^a Additional plant species encountered or species that were aggregated to genus for forage selection analyses include *Actaea rubra*, *Aira caryophylla*, *Amsinckia menziesii*, *Chrysosplenium glechomaefolium*, *Collomia heterophylla*, *Coptis asplenifolia*, *Corydalis scouleri*, *Dicentra cucullaria*, *Festuca* spp., *Fragaria virginiana*, *Galium aparine*, *Geranium robertianum*, *Geranium* spp., *Gnaphalium microcephalum*, *Goodyera oblongifolia*, *Habenaria dilatata*, *Lathyrus sylvestris*, *Ledum groenlandicum*, *Listera cordata*, *Lithophragma parviflora*, *Lupinus latifolius*, *Malus fusca*, *Medicago lupulina*, *Nemophila parviflora*, *Pachistima myrsinites*, *Polygonum bistortoides*, *Habenaria dilatata*, *Lathyrus sylvestris*, *Ledum groenlandicum*, *Listera cordata*, *Lithophragma parviflora*, *Lupinus latifolius*, *Malus fusca*, *Medicago lupulina*, *Nemophila parviflora*, *Pachistima myrsinites*, *Polygonum bistortoides*, *Psoralea physodes*, *Pyrola* spp., *Ranunculus repens*, *Ranunculus uncinatus*, *Rosa nutkana*, *Salix scouleriana*, *Sambucus cerulea*, *Sambucus racemosa*, *Senecio jacobaea*, *Senecio* spp., *Stellaria calycantha*, *Stellaria crispa*, *Stellaria simcoeii*, *Stipa* spp., *Symphoricarpos albus*, *Symphoricarpos mollis*, *Vaccinium ovatum*.

^b Plant group codes are Cn = conifer; Fb = forb; ES = evergreen shrub; DS = deciduous shrubs; Fn = fern; Gr = graminoid; NV = non-vascular.

^c No measure of abundance was sampled and thus no estimates of selection could be calculated. The selection category was based on authors' general observations of elk response to this species. Sample size and dietary percents were based only on those elk pens where the species was present in their diet (and thus dietary percents may be overestimated).

^d For attached leaf lichens, we are referring to those leaf lichens attached to trees and include numerous genera and species (Pojar and MacKinnon 1994).

APPENDIX F. Composition of plant species in elk diets and in plant communities at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Data are pooled among study areas and presented for early seral and closed canopy forests in the western hemlock-salal and -swordfern habitat types, and combined across successional stages for the Pacific silver fir and mountain hemlock habitat types. Open bars represent composition of plant species available to foraging elk and black bars the composition of species in elk diets. Within each habitat type-stand age category, all plant species either >1% available or species >1% of elk diets are presented. Percent composition of plant species in plant communities (available) was calculated in macroplots with elk foraging where dietary composition (used) was sampled. Four-letter plant codes are defined in Appendix E.

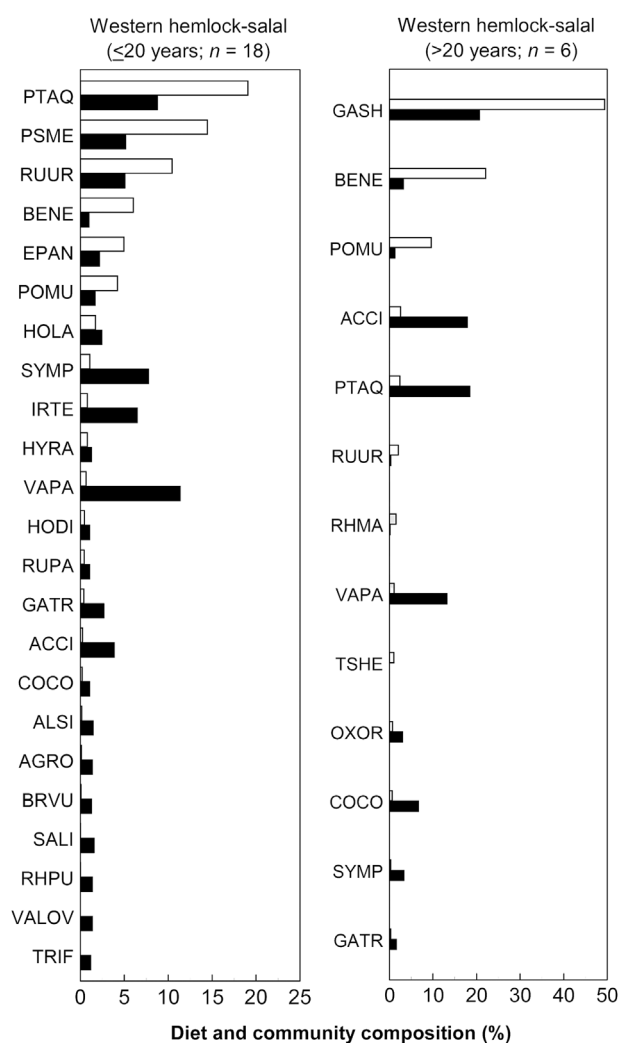


Figure F1. Percent use by elk and percent available of plant species composing either ≥1% of elk diets or community composition in western hemlock-salal habitat type at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

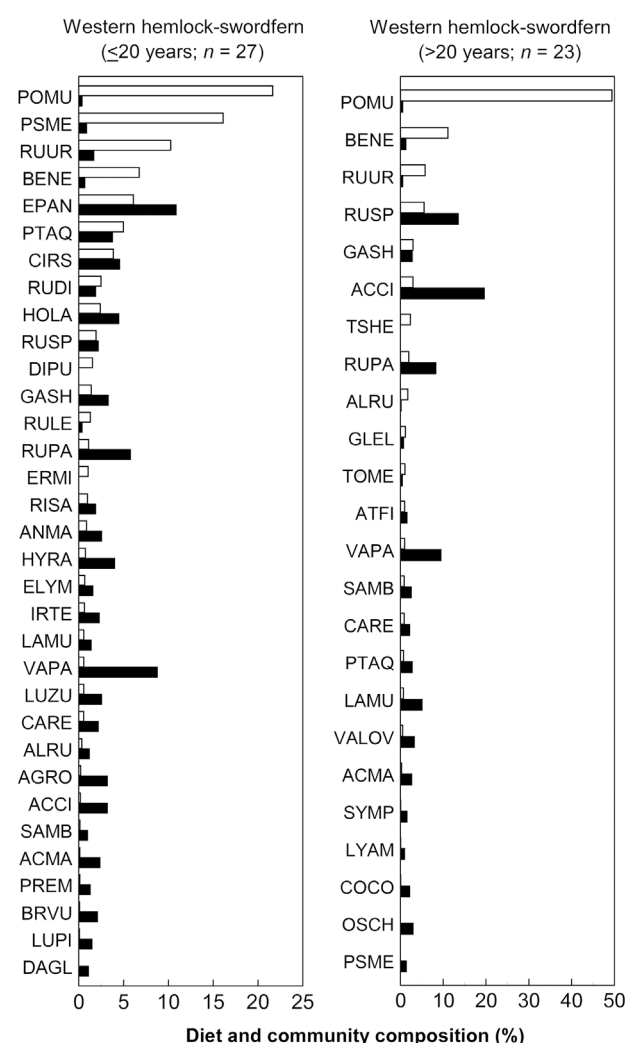


Figure F2. Percent use by elk and percent available of plant species composing either ≥1% of elk diets or community composition in western hemlock-swordfern habitat type at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

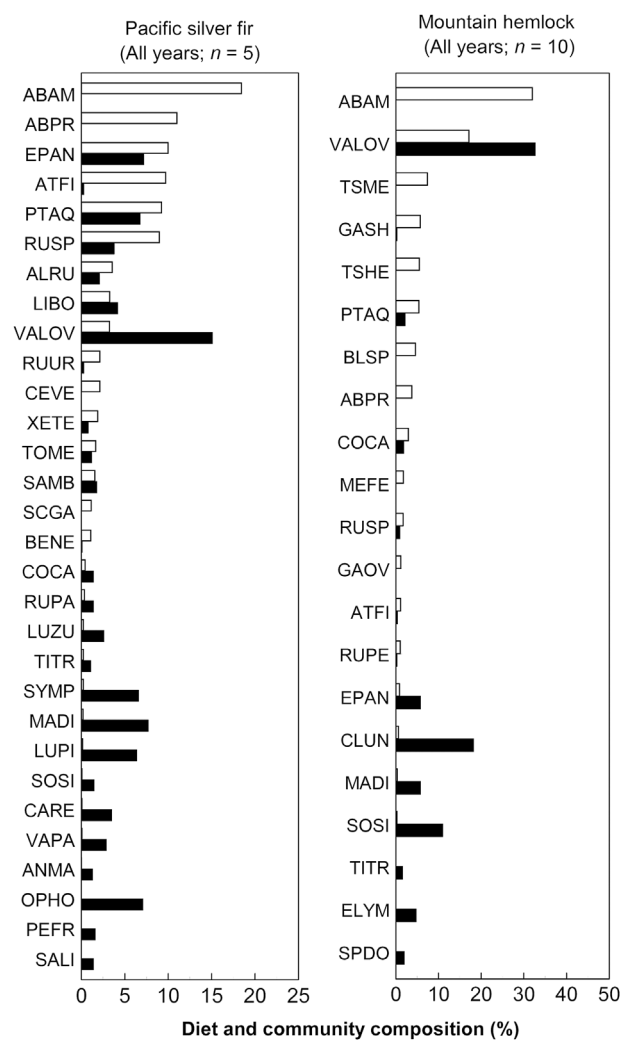


Figure F3. Percent use by elk and percent available of plant species composing either $\geq 1\%$ of elk diets or community composition in Pacific silver fir and mountain hemlock habitat types at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002.

APPENDIX G. Abundance of species accepted by elk and all plant species by habitat type across succession at Nooksack, Willapa Hills, and Springfield study areas in western Oregon and Washington, 2000–2002. Data from thinned (including those in Pacific silver fir and mountain hemlock habitat types) and hardwood macroplots are presented separately.

